

The Genus *Tremogasterina* Canu (Bryozoa, Cheilostomata)

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Synopsis

The development of the general concept of the characters of the genus *Tremogasterina* is discussed, and a summary of the character correlations now considered to be typical of the genus is given. The astogeny of the colony, and the ontogeny of the umbonuloid frontal shield and secondary calcified orifice is described, together with observations of the ontogeny and astogeny of the avicularia and brood chambers (ovicells). Analysis of populations indicates that two divergent trends in zooid and colony structure may

have been evolved since the Paleocene. Fifteen nominal species or populations are described, from the Paleocene to the Recent, and their distribution in time and space is discussed. Two new species are described. The nomenclature and affinities of the genus are discussed. The nature of the frontal shield ontogeny raises problems in recognition and interpretation, particularly of fossil specimens; further fields of work are suggested which may provide some solutions.

Introduction

The concept of the genus '*Tremogasterina*' has been well defined from Recent and late Tertiary fossil specimens and its characters are distinct. Unfortunately, there are problems both in the interpretation of the type-species, and in the priority of the name itself. The history of *Tremogasterina*, and of the related genus *Poricella*, is discussed on p. 125. Setting aside the nomenclatorial problems, the name *Tremogasterina* is used here for a group of species having umbonuloid frontal shield ontogeny, frontal foramina, large secondary calcified orifices with oral spines, interzoooidal brood chambers ('hyperstomial ovicells', see p. 124), and both interzoooidal and vicarious avicularia, with mandibles slung on a complete bar or from paired condyles.

Powell & Cook (1967) showed that the characteristic foramina in the calcified frontal shield, from which the generic name was derived, could be reduced or even completely occluded during ontogeny, but that a foramen was present at least during the early ontogenetic stages. The present study illustrates the considerable morphological diversity resulting from different developmental series of one basic type of frontal shield ontogeny within the complex of species nominally assigned to *Tremogasterina*.

The anasciform affinities of *Tremogasterina* have resulted in its having been regarded as belonging to the Anasca (Bassler, 1953) and to the Ascophora Imperfecta (Harmer, 1957). Several of the forms included by Harmer in the 'Ascophora Imperfecta' do not have umbonuloid frontal shield development, and the two concepts are not necessarily the same. In the Petraliidae, Petraliellidae and Celleporariidae, for example, the ontogeny of the frontal shield shows similarities with both the cryptocystidean and umbonuloid types of development. The probability of other forms of ontogeny also requires further investigation. In fact, the number of species which have been studied in detail is so small that the assumption that a few major systematic divisions may be made on these grounds alone is almost certainly premature. On the other hand, the known differences in developmental episodes, and in their sequence, and the differences in the homology and morphology of the layers involved are apparently so important that it seems equally certain that they reflect the evolution of polyphyletic groups. The similarity in appearance among the late ontogenetic stages indicates a considerable degree of convergence and parallel development among the major groups now included in the Cheilostomata (see also p. 123).

The existence of at least two distinct methods of formation of a calcified frontal shield and related hydrostatic apparatus in some Cheilostomata has now been demonstrated in some detail (see Banta, 1970, 1971; Cook, 1973). Studies of living species and the application of hard/soft sectioning techniques have shown that although the later ontogenetic stages may appear very similar, there is a series of fundamental and correlated differences between the two methods of frontal shield calcification and hydrostatic apparatus formation.

In cryptocystidean growth the calcified layer is an interior partition wall and develops before the operculum is differentiated completely. It grows distally into a coelomic space until the primary calcified orifice is delineated. A sacciform ascus, which comprises the hydrostatic apparatus, is then formed by invagination from a group of cells proliferating from the proximal edge of the operculum. In the late stages of ontogeny, the calcified internal wall has no coelomic space on its basal side in the majority of species examined. A cryptocystidean frontal shield which remains surrounded by coelome basally and frontally is, however, known in *Tropidozoum* (see Cook, 1975).

In umbonuloid growth a frontal fold grows in a distal direction, frontally, above a previously formed anasciform frontal membrane. The operculum and parietal muscles are differentiated at an early stage in the ontogeny of the fold. The fold is calcified on its basal side only, leaving a space basally, between the fold and the frontal membrane. On the upper, frontal side of the calcified layer of the fold, there is a hypostegal coelome which communicates with the visceral

coelome by means of marginal frontal septulae. The calcified layer eventually forms a secondary calcified orifice in apposition to, but above, the uncalcified primary orifice and operculum. The space between the frontal membrane and the calcified frontal shield forms the hydrostatic apparatus, and is functionally identical with the cryptocystidean ascus. Morphologically, however, it is similar to the epistegal space of the Cribrimorpha, and this term is used here, in order to emphasize the differences between the two forms of development.

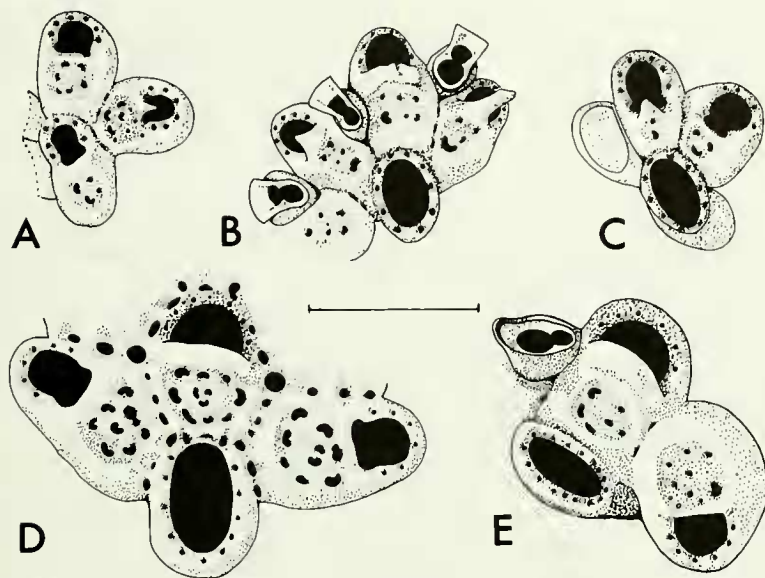


Fig. 1 Ancestrulae and primary zooids of *Tremogasterina*. Sketches showing orifices, spine-bases and frontal foramina; details sometimes based on more than one specimen. (A) *T. perplexa* Cook, Ghana, BMNH, 1973.3.22.27. Ancestrula probably missing, zooids on left damaged. (B) *T. spathulata* (Canu & Bassler), East Indies, BMNH, 1961.10.30.8.9. Note prominent apertural bar and distally descending orifice of distal primary zooid. Avicularia have been budded between primary and secondary zooids. (Spine-bases from another specimen.) (C) *T. oranensis* (Waters), Senegal, BMNH, 1970.8.10.9A (with *Membranipora arborescens*). Note large orifice of primary distal zooid; zooid on left has not developed normally. (D) *T. robusta* (Hincks), Red Sea, BMNH, 1965.8.8.8. Note large size, coalescence of areolae to form funnels, and apertural bar and distally descending orifice of primary distal zooid. (Spine-bases from another specimen.) (E) *T. mucronata* (Smitt), Gulf of Mexico, BMNH, 1961.11.2.41. Note apertural bar and distally descending orifice of primary distal zooid. (Avicularium from another specimen.) Scale = 0.50 mm.

Abbreviations and terminology

Length of zooid	Lz	Width of zooid	lz
Length of orifice	Lo	Width of orifice	lo
Length of brood chamber	Lov	Width of brood chamber	lov
Length of rostrum of interzooidal avicularium	Lr	Length of rostrum of vicarious avicularium	Lvic
BMNH	British Museum (Natural History) Collections		
USNM	United States National Museum Collections		
NMV	Naturhistorischen Museum, Vienna Collections		
UCB	Université Claude Bernard, Lyon Collections		
USC	University of Southern California Collections		
MAC	Musée Royale de l'Afrique centrale, Tervuren Collections		
UMC	Universitetets Zoologiske Museum, Copenhagen Collections		

BROOD CHAMBER – the chamber in which the embryo is brooded. In *Tremogasterina* the chamber is exterior and has calcified walls and the term is equivalent to 'ovicell'. In many other cheilostomes the brood chamber is a diverticulum from the exterior, housed within the zooid walls, and may or may not have calcified walls.

EPISTEGAL SPACE – the space between the uncalcified frontal wall and the basal side of the frontal shield in umbonuloid and cribrimorph cheilostomes.

FRONTAL SHIELD – the cheilostome frontal wall with calcified skeleton – formed by an interior partition wall in cryptocystidean groups, by an external, basally calcified fold in umbonuloid groups, and by a series of external, calcified spinous processes in cribrimorph groups.

PRIMARY ORIFICE – the cheilostome orifice which is protected by the operculum – calcified in cryptocystidean forms, uncalcified in umbonuloid forms.

Astogeny

The early colony development is known in *Tremogasterina robusta*, *T. spathulata*, *T. oranensis*, *T. mucronata* and *T. perplexa*. In the first four species the ancestrula is membraniporiform, in the last it may perhaps be similar to succeeding zooids.

The ancestrula and early budding of *T. robusta* was described by Powell & Cook (1967). Specimens (BMNH, 1965.2.4.11, 1965.8.8.8., Massawa, Red Sea underneath oyster scutes) have from ten to eighteen long spines overarching the ancestrular opesia, and two to three primary zooid buds. The buds have six spine bases and eight to eleven frontal foramina. The ancestrula of *T. spathulata* was described by Harmer (1957 : 658). Specimens (BMNH, 1961.10.30.8 and 9, East Indies, Siboga Coll.) have ten spines and three distal zooid buds. The buds have six spines and four to six frontal foramina. Interzooidal avicularia arise between both the first and second generation zooids. The ancestrulae of *T. oranensis* (BMNH, 1970.8.10.9B, Senegal, on shell with *Membranipora arborescens* and many other species) are larger than the subsequent zooids and have a well-developed proximal gymnocyst, eight to ten spines and two to three distal or lateral and distal buds. The buds have four to six spines and two to four frontal foramina. The ancestrula of *T. mucronata* (BMNH, 1961.11.2.41, Campeche Bank, Gulf of Mexico) has sixteen spines and two primary buds. The buds have six spines and five to ten frontal foramina. Another colony, from which the ancestrula is missing, has a small, proximally orientated avicularium between the primary buds; the mandible is rounded, not truncate and distally expanded as in succeeding avicularia. The primary zooid of the colony of *T. perplexa* (BMNH, 1973.3.22.27, Ghana) is slightly damaged and may not in fact be the ancestrula. It is smaller than the next two distal zooids and has a calcified orifice with approximately six spines; there are four frontal foramina. The distal zooids have six spines and four to nine frontal foramina.

In all cases the primary buds are produced distally or distal-laterally. In several species the central distal bud in particular, has a larger secondary calcified orifice than the other zooids. The orifice descends rapidly distally, and there is a prominent suboral apertural bar, similar to that of many cribrimorphs, and to the zooids of *T. maçonica* (see pp. 121, 128).

The primary buds, and to a lesser extent the zooids in the primary zone of astogenetic change of all species, are strikingly similar in appearance (see Fig. 1A–E). All have a distinct, slightly depressed frontal area with several small lunate or irregular frontal foramina which are not occluded by subsequent calcification. Both foramina and oral spines tend to be more numerous than in zooids in the zone of astogenetic repetition.

The majority of Recent and fossil species encrusts shell (frequently oyster shell), coral, Bryozoa and calcareous concretions. *T. mucronata*, *T. celleporoides* and *T. robusta* tend to form erect, unilaminar or occasionally loosely bilaminar and tubular expansions, arising from an encrusting base. *T. maçonica*, *T. areolata*, *T. spathulata*, *T. perplexa* and *T. musaica* are entirely encrusting and form far smaller colonies. *T. oranensis* and *T. brancoensis* are primarily encrusting, but become erect with long tubular branches later in their astogeny. *T. brancoensis* also develops truly bilaminar branches. In nearly all species the primary zone of astogenetic repetition is followed by one or more secondary zones of overgrowth. These overgrowths arise from a focus of one or two

zooids, and grow in all directions. In *T. celleporoides*, *T. oranensis* and *T. brancoensis*, several sequential overgrowths occur, and one or more distinct growing edges may be seen to form the erect branches or lobes.

Generally, it appears that umbonuloid forms do not produce multilaminar colonies by colony-wide frontal budding, as described for some cryptocystidean forms such as those studied by Banta (1972). The presence of a hypostegal coelome in umbonuloid species makes it hypothetically possible for frontal buds to be produced, and in *Tremogasterina* the primary zooids initiating overgrowth do develop in this way. They are apparently derived from frontal septulae, which are covered by cuticle and epidermis. In thin-section it can be seen that the basal walls of the overgrowth zooids are frequently not in contact with the frontal shields of the overgrown zooids. The primary frontal bud forming an overgrowth develops later in the astogeny, but in a similar manner to the interzooidal avicularia. It is derived from the frontal septulae of adjacent zooids and in some specimens (e.g. *T. celleporoides* BMNH, 1961.10.30.16, see Pl. 1A and *T. mucronata* BMNH, 1911.10.1.1698) a row of marginal funnels (common to both zooids at this ontogenetic stage) can be seen to open into the basal side of the bud. In another specimen of *T. mucronata* (BMNH, 1931.5.2.6) there is a group of several deformed frontal buds. They arise interzooidally above the space separating adjacent zooids and extend vertically above the surface of the colony. Development was not complete at death, and these zooids may never have been able to develop normally. They are calcified on the distal (normally basal) side, and have a membranous wall on the proximal (normally frontal) side. These colonies also have dimorphic zooids (see p. 131), and may have been reacting to some unknown microenvironmental influence.

The normal frontal bud produces a triad of distal and distal-lateral zooids, in a similar pattern to that produced by the ancestrula (seen in *T. spathulata*, BMNH, 1965.9.4.1, Red Sea and many colonies of *T. oranensis*). Overgrowths later bud in all directions, and the erect, tubular branches of *T. oranensis* and *T. celleporoides* are frequently formed of several layers, some growing proximally, others laterally and distally.

Zooids of overgrowth zones are sometimes affected by microenvironmental influences especially at the earlier stages, and may be irregular in shape, but generally there appears to be little or no difference between them and the zooids of the primary zone of repetition.

Ontogeny of zooid walls

The frontal calcified shield and hydrostatic apparatus

As in other umbonuloid forms observed (see Cook, 1967, 1973), the ontogenetic changes appear to occur as a series of rapid episodes, alternating with periods of slower development. Colonies showing complete ontogenetic series are therefore rare, but zooids observed from several colonies from the same sample will usually provide information enabling all the developmental episodes to be traced. Equally complete series have not been available in all the species examined, but the ontogeny appears to follow the same general pattern (see Figs 2, 3).

Zooids at the growing edge nearing their full length possess calcified basal and lateral walls, and a partially calcified distal transverse wall at least. Uncalcified buds extending distally to partially calcified zooids do not occur very often, and suggest that, as in *Exechonella*, budding occurs in distinct episodes, rather than the continuous process found in, for example, *Membranipora membranacea* (see Lutaud, 1961). Distal and lateral septulae are present in the calcified walls and the frontal wall is entirely membranous. It is considered here that the lateral and distal walls do not develop further, i.e. that there is no further potential surface of direct contact among visceral coelomes of zooids in a primary zone of change or repetition after this stage in the ontogeny. Upward (i.e. frontal) growth from this stage may appear to be a continuation of the lateral and distal walls, and to be indistinguishable, using a light microscope, from that which preceded it, but is here regarded as frontal wall development. Additional contact among zooids is therefore entirely among hypostegal coelomes.

The calcification proceeds as a continuous, curved lamina which extends from the proximal to the distal end of the zooid. The lamina begins to turn inward, the most rapid development being

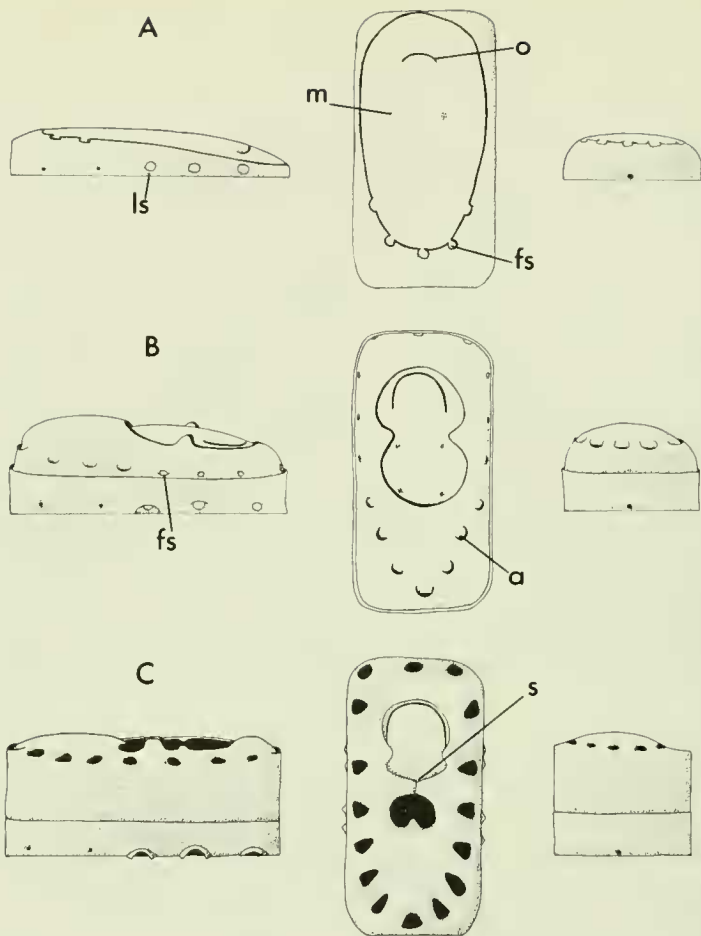


Fig. 2 Early ontogeny of the vertical and frontal walls in *Tremogasterina*. From left to right, diagrams are of lateral, frontal and proximal views of a zooid (see also Fig. 3). (A) Establishment of general basal extent of zooid by lateral calcified vertical walls. Note lateral septulae (*ls*) and incipient frontal septulae (*fs*). Differentiation of the operculum (*o*) and parietal muscles (*m*) has commenced. (B) Overarching of uncalcified frontal wall by umbonuloid fold over epistegal space. Note that thickening of calcification has already produced 'areolae' (*a*) above the proximal frontal septulae. Note that much of the upper part of the 'distal wall' is formed by the incurved transverse frontal fold. Primary (uncalcified) orifice is complete, secondary calcified orifice not yet formed. Lateral septulae developing overarching buttresses of calcification. (C) Early stage of secondary calcified orifice and foramen. Note sutures between processes forming apertural bar above opening of epistegal space. Lateral indentations of orifice are frontal to developing condyles. Note thickening of calcification and complete areolae. Lateral septulae now surrounded by chambers.

proximally and laterally. At the same time a series of multiporous frontal septulae are developed, which usually extend from the proximal to the distal end of the zooid (see Pl. 1A). A ridge of calcification develops just below the septulae, perhaps indicating the division between the lateral and distal transverse walls, and the frontal lamina. Studies on, for example, the ultrastructure of the walls may show further evidence of changes in crystal structures at this point. At this stage the uncalcified frontal wall shows the beginning of the differentiation of the operculum (see Fig. 2A). The calcified lamina above the ridge may be regarded as the basal part of a double-layered expansion, the upper (frontal) part of which is uncalcified. The double-layered expansion evaginates above the primary uncalcified wall which then can be regarded as the equivalent of an anasciform frontal membrane, including the operculum and developing parietal muscles. As calcification proceeds and both layers overarch the frontal membrane, they leave an epistegal space on their basal side (Cook, 1973, and Fig. 2B, C). It is inferred that the upper layer of the shield consists of an expansion of cuticle and epidermis above a hypostegal coelome which is in contact with the visceral coelome through the frontal septulae (see Fig. 2B). Both layers continue to develop in an umbonuloid manner above the frontal membrane, in which the operculum and frontal parietal muscles are completely differentiated.

The operculum is very thick and closely apposed, but not attached, to the secondary calcified orifice which is delineated by the anastomosis of paired distal processes in the calcified lamina (see Fig. 2C). This development is similar to that seen in *Tripurula* and *Exechonella*, and in the Adeonidae (see Cook, 1967, 1973).

The development of the secondary calcified orifice is accompanied by thickening of the frontal calcification and the obscuring of the frontal marginal septulae by intervening calcified buttresses which extend upward into the hypostegal coelome. The buttresses close frontally, forming tubes in the calcification which open into the hypostegal coelome frontally, and are in contact with the frontal septulae and therefore with the visceral coelome basally (see p. 110). These tubes are 'areolae' (see Banta, 1973), and may develop further (see p. 111).

The primary frontal foramen is formed at the same time as the secondary orifice by the anastomosis of the lateral distal calcified processes (see Fig. 2C). It is usually subdivided by extension and fusion of further processes into three to four smaller foramina. These may become further subdivided by unilateral processes which project into the cavities, making them lunate or reniform. These processes themselves may bear spinules. The larger foramina may remain open, but in many cases, cuticle extends across them basally and frontally, making them uncalcified 'windows' continuous internally with the hypostegal coelome. Subsequent calcification may thicken the frontal shield considerably, and occlude or obscure the foramina (see below, pp. 111, 135), and the secondary orifice may become depressed. The area proximal to the orifice frequently becomes mucronate (see Fig. 3 and Pl. 6E). In many fossil and Recent specimens the mucro is broken or worn; the extent of growth possible is shown by specimens of *T. mucronata* collected by divers *in situ* from a submarine cliff face at 60 metres depth off northern Jamaica. The mucros of these colonies reach 0.25 mm in length and are bifid or trifid; they may be uncalcified terminally and were covered by thick cuticle. In *T. perplexa* (see p. 138) the entire frontal may develop a prominent, hollow median keel, which obscures the frontal foramina (see Pl. 1E). Conversely, the central part of the shield may not be thickened, and the foramina then become depressed in a distinct area. This occurs in *T. mucronata*, *T. celleporoides* and *T. areolata* (see also Osburn, 1950 : 98, and Pl. 1C).

The form and eventual extent of thickening is closely connected to the development of interzooidal and extrazooidal intercommunication of hypostegal coelomes (see p. 111). It is a resultant of the multivariate effects of ontogenetic age, astogenetic position, microenvironmental and environmental factors and the genetic structure of the colony.

Zooidal communications

All zooids communicate through multiporous septulae in the distal and lateral walls. Species of *Tremogasterina* are frequently stated to possess diatellae (pore chambers), and in some colonies (notably of *T. celleporoides* and *T. robusta*) they certainly appear to be present (see also Powell &

Cook, 1967). Further examination of specimens, however, has shown that there are several problems involved in the determination of diatellae which require further investigation. Recent work by Banta (1969), Gordon (1971) and Harmelin (1973) has emphasized the need to study the complete ontogeny of intercommunication structures, not just the end product. Gordon remarked (1971 : 460), 'Distinctions between diatellae exist in different groups, especially in their mode of formation.' Some of the diatellae mentioned by Gordon differed in the calcification sequences. In *Fenestulina* the outer and inner (pore plate) walls of the diatellae calcified 'more or less simultaneously', whereas in *Callopora*, as described by Silén (1944) and in *Crassimarginatella* as described by Harmelin (1973), the inner pore plate wall calcified after the outer wall. In both examples, the formation of the diatellae took place within the primary sequence of zooidal calcification. In *Tremogasterina* the formation of the outer wall of the chamber takes place, if at all, far later in the ontogeny. Multiporous septulae are formed as the lateral and distal transverse walls calcify. The next generation of zooid buds is then formed as an expansion of cuticle, epidermis and coelomic tissue from the pore plate of the septulae. It is only after the partial calcification of the zooidal walls of this bud that the formation of a calcified chamber surrounding the parent septula may occur as a distinct episode. In many colonies, and in zooids within colonies, no chamber is formed, the extra calcification being confined to intervening buttresses between septulae, especially those in the lateral walls. Generally, the distal septulae become surrounded by a distinct chamber, but in most specimens the 'pore' which leads into the distal zooid remains very large. In the *T. spatulata* group the pore may become a horizontal slit, and this development sometimes occurs in *T. oranensis*. The differences among diatellae, and between them and 'buttressed' or 'chambered' pores (see Cook, 1964 : 16), may thus be alternately interpreted as fundamental differences in ontogenetic sequence, or as stages in the evolution of distinct and complex structures (see also Harmelin, 1973 : 478 *et seq.*). The end products of these developmental series may appear to be identical, but if there are any real differences, these can only be recognized when a complete ontogenetic series is present. It seems that the term 'diatella' or 'pore chamber' should be used with caution until the ontogeny of a far greater range of species has been investigated (see also p. 124).

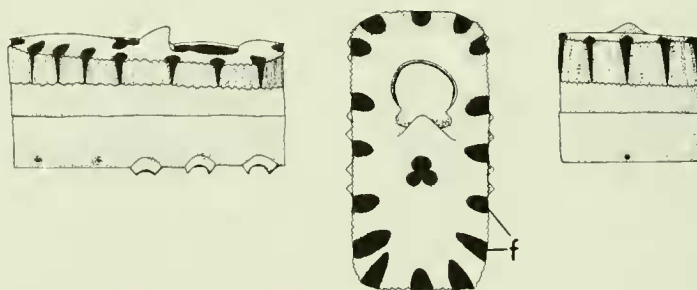


Fig. 3 Late ontogeny of vertical and frontal walls in *Tremogasterina*. (Sequence of diagrams as in Fig. 2.) Development of extrazooidal thickening and enlargement and coalescence of areolae to form funnels (f) between adjacent zooids. Note suboral mucro and further development of chambers around lateral septulae.

Both distal transverse and lateral walls are in fact very shallow, and the distal transverse wall may consist of little more than the area surrounding the distal septula. The remaining, more frontal, part of the apparent distal wall consists of the slightly inturred, distal part of the frontal umbonuloid fold. This explains the presence of cuticle traces between zooids seen in longitudinal sections. Thickening is so rapid that in frontal view, and in some sections, the calcified part of the fold may appear continuous with the distal transverse wall. In a pair of sequentially budded zooids the tubes in the calcification forming the areolae derived from the distal frontal septulae of the proximal zooid, and those from the proximal frontal septulae of the distal zooid usually

combine their cavities during thickening to form a single marginal 'funnel' in frontal view. In some colonies this occurs early in ontogeny. Similarly, the lateral frontal areolae from lateral septulae of adjacent zooids form joint funnels, as noted by Osburn (1950 : 98). The development of the brood chamber is closely related to the resultant continuity of hypostegal coelomes of both sequential and adjacent zooids (see p. 114). The coelomic connection beneath the cuticle and epidermis during later stages of ontogeny results, in some colonies, in extrazoidal thickening of the calcification in which zooidal contributions merge and become colony-wide (see also Cheetham, 1968 : 11, and Fig. 3). The transfer of nutrients to the hypostegal coelome by the frontal septulae make them the potential site of interzooidal avicularia, brood chambers and frontal buds. In *T. spathulata*, incipient frontal avicularia also arise from frontal foramina which, in this species, are closed by cuticle basally and frontally (see p. 109). The laterally placed frontal septulae are large and the calcified funnels surrounding them persistent in late ontogeny, in most species, both fossil and Recent. In the *T. spathulata* group, however, they are extremely small, and it may be possible that this is correlated both with the number and nature of the frontal foramina. In ontogenetic thickening of the calcification, these foramina themselves develop as calcified funnels which extend until they are in contact with each other and then thicken frontally forming 'blocks'. The formation of blocks of calcification is particularly well developed in *T. musaica* (see Pl. 1F), and greatly resembles that found in the later ontogenetic stages of *Exechonella*, which also has minute frontal septulae. In the *T. spathulata* group the foramina are 'windows', and are closed basally and frontally by cuticle. They are thus in contact with the hypostegal coelome directly. Due to their large numbers and extent they effectively increase the thickening of the whole frontal calcified wall. In other species, where the foramina are reduced in number, or remain open, thickening is produced by the whole frontal epidermis supplied by nutrients through the frontal septulae.

Oral spines and oral condyles

Spines are present in nearly all species and develop as small invaginations and anastomoses in the distal part of the calcified lamina of the frontal fold as it overarches the operculum. They therefore develop fairly late in the ontogeny (see p. 122). Generally, the bases of the spines are cuticular. Spine-base scars are often obscured by later calcification, but may remain distinct (see Pls 1C, F and 5B, E). Condyles develop as shallow, basally directed grooves in the lamina at the sides of the secondary calcified orifice. The inner edges of the grooves thicken and form the lateral indentations visible frontally in many specimens. Further, secondary, basally directed extensions of the calcification below the lateral indentations form the inner condyles, which are often not visible frontally. In some specimens condyles are not apparently formed. When present, they extend and insert below the lateral edges of the operculum, on the proximal side of its transverse mid-line when open, so that it becomes pivoted between the two sets of calcified processes on each side. It must be remembered that the operculum is capable of opening, and the zooid of feeding, before the completion of the frontal calcified shield in umbonuloid forms (see Cook, 1973 : 249). The condyles and lateral indentations presumably ensure that the operculum remains closely apposed beneath the thickening calcification of the secondary orifice. The occlusor muscles are very large and are inserted into the distal half of the operculum. They run vertically and slightly distally to the condyles and are inserted into the distal wall and distal part of the lateral walls near their bases. The divaricator muscles are attached to the proximal part of the operculum and are inserted in the upper part of the lateral walls.

Ontogeny and astogeny of the avicularia

Avicularia arise variously, in some species early in zooidal ontogeny. For example, in *T. mucronata* and *T. oranensis* avicularia are budded regularly between zooids, forming alternating series laterally (see Pl. 6 and 7C), and development begins as soon as the zooid frontal shields have calcified. In *T. celleporoides* position and orientation of avicularia are usually much more variable,

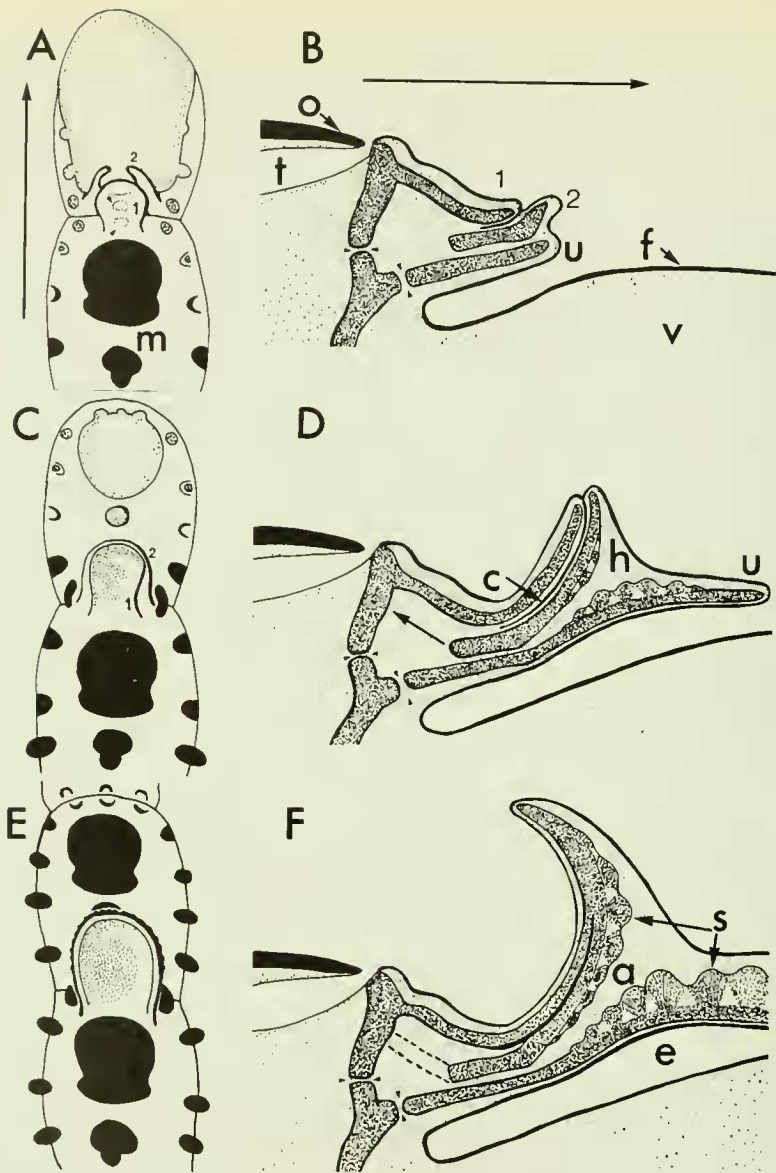


Fig. 4 Ontogeny of brood chamber. A, C, E, diagrammatic sketches of frontal appearance of brood chamber development. Cuticle omitted, direction of colony growth arrowed. D, B, F, diagrams of longitudinal sections through developing brood chamber at comparable stages; not to the same scale as A, C, F. Cuticle black, coelome light stipple, calcification dark stipple. Direction of colony growth arrowed. Distal frontal septulae of maternal zoid and proximal frontal septulae of distal zoid indicated by small arrows.

(A) Maternal zoid (*m*) with small distal lamina (1) growing distally into common hypostegal coelome expansion between maternal zoid and distal zoid (surrounded by cuticle in life). Frontal fold of distal zoid has developed crescentic outer brood chamber lamina (2) in the same way. (B) Longi-

and development does not begin until two or three zooid rows have developed fully. The subrostral chamber first appears to develop from extensions of the buttresses between areolae and as a calcified funnel, covered by cuticle. The bud derives from two or more zooids and is thus interzooidal. The rostrum and calcified bar or condyles grow beneath the cuticle, in which the mandible is differentiated in a similar manner to that of the zooidal operculum. Mandibles may be slung on a complete calcified bar, or from paired condyles; there is a good deal of intraspecific variation among populations, and even among colonies in this character. In fossil specimens, the bar is often broken and appears as paired condyles.

Mandibles and rostra also show intraspecific variation, particularly within the *T. mucronata*-complex and in *T. spathulata*. In addition the shape of the rostrum in fossil specimens may be altered by preservation or wear. The character of mandible shape is, however, fairly specific; for example in *T. robusta* mandibles are usually asymmetrical, and in *T. musaica* small and acute. In *T. lanceolata* the elongation of the mandibles is such that it apparently restricts the development of the calcified frontal shield of the next distal zooid (see also Powell & Cook, 1967). The *lanceolata*-form of growth also occurs, however, in some colonies of *T. mucronata* and *T. robusta*, particularly where the zooids and avicularia are budded in lateral rows, like the zooids of *Electra verticillata*. 'Verticillate' growth also occurs in some colonies or parts of colonies of *T. celleporoides*, but here the rounded shape of the mandibles precludes any *lanceolata*-form of frontal wall development. 'Verticillate' growth is often found in erect, unilaminar or tubular portions of colonies, but may also occur in encrusting expanses; the avicularia are almost without exception orientated distally in these colonies. Orientation of mandibles is also conspicuously distal in some species (e.g. *T. robusta* and *T. oranensis*), and lateral or random in others (e.g. *T. spathulata* and *T. celleporoides*). Nevertheless, there is also a great deal of intraspecific variation in populations of *T. spathulata* and *T. mucronata*, and in *T. brancoensis* there is a correlated change in mandible shape and orientation which is related to the geographical distribution of the populations (see p. 134). Interzooidal avicularia occur very early in the astogeny of *T. spathulata* and *T. mucronata*, arising between the first or the first and second generation zooids (see Fig. 1). In *T. robusta* and *T. oranensis* they have not been found to occur before the third and fourth zooid generations.

Vicarious avicularia are known in most species and arise among the zooids, communicating with them through lateral and distal septulae. They are a feature of overgrowth layers, often occurring in groups. In most species the rostra and mandibles are similar to those of the interzooidal avicularia, but in *T. brancoensis* they are dissimilar in the two forms. In *T. mucronata*, some colonies have dimorphic zooids, closely similar to vicarious avicularia, but with frontal foramina (see p. 131).

The frequency of occurrence of both interzooidal and vicarious avicularia varies considerably among the species. For example, the proportion of interzooidal avicularia to zooids in *T. brancoensis* is 3 : 2, in *T. areolata*, *T. mucronata*, *T. subspatulata*, *T. robusta*, *T. celleporoides* and *T. oranensis* it is approximately 1 : 1, in *T. spathulata* and *T. musaica* it is 1 : 2, and avicularia are

tudinal section at a slightly later stage than (A), after fusion of the horns of the crescentic lamina (2), frontal to the calcified part of the developing umbonuloid fold (*u*) of the distal zooid, from which it is derived. (1) lamina from maternal zooid, (*o*) operculum of maternal zooid, (*t*) cavity of tentacle sheath of maternal zooid, (*f*) cuticular frontal wall (frontal membrane) of distal zooid, (*v*) visceral coelome of distal zooid. (C) Further development of both laminae. Note proximally directed extension of distally derived lamina (2) to meet distal part of maternal zooid frontal fold. (D) Longitudinal section at same stage as (C). Direction of proximal extension of lamina (2) which is out of section, arrowed. Note imminent fusion of two laminae terminally and the 'pinching out' of the coelomic cavity between them, leaving a cuticle trace (*c*). (*h*) hypostegal coelome, (*u*) distally migrating edge of umbonuloid fold of distal zooid. (E) Brood chamber after fusion of laminae and further frontally directed growth. (F) Longitudinal section at same stage as (E). Secondary calcification developing on outer surface of brood chamber (cf. Pl. 8C), and on frontal shield of distal zooid (*s*), (*a*) areola leading to frontal septula, (*e*) epistegal space of distal zooid. Position of proximal extension of lamina (2), which is out of section, indicated by dotted lines.

absent in *T. perplexa*. Vicarious avicularia are common in *T. celleporoides* and some populations of *T. brancoensis*. They are frequent in some colonies of *T. spathulata* and *T. oranensis*, rare in *T. robusta*, and apparently absent in *T. perplexa*, *T. musaica* and *T. lanceolata*.

Ontogeny and astogeny of brood chambers (ovicells)

The development of brood chambers varies in sequence of episodes and in the relative rate and timing of sequences both within and among colonies and species. It has been traced by observation of growing regions of colonies, including examination of thin-sections and by scanning electron microscopy. Specimens of two species, *T. mucronata* (BMNH, 1931.5.2.6) and *T. celleporoides* (BMNH, 1890.3.24.34 and 1961.10.30.16), have shown almost complete sequences of development, and the following reconstruction of the ontogeny is based upon them. Isolated episodes have been seen in colonies of these and other species which allow the inference that the process is fundamentally the same throughout the genus.

Two basic factors in understanding the ontogeny are the contact among zooids of hypostegal coelomes across the colony surface, and the rapid and continuous thickening of the frontal shield calcification which occurs simultaneously with brood chamber development. Episodes in the ontogeny are illustrated in Pl. 2 and Fig. 4.

Brood chambers are usually developed near the growing edge, but may not begin to develop until a later stage in colony astogeny. None can develop until the zooid which will produce the ovum (the 'maternal zooid', see Cook, in press) has the primary frontal shield development complete, and the next sequential, distally placed zooid or zooids have at least the proximal part of their frontal shield or shields calcified and their frontal septulae formed.

The first sign of development visible in untreated specimens is a small, flattened expansion of cuticle on the descending part of the frontal shield of the maternal zooid, distal to the newly formed secondary calcified orifice. This is an expansion of the frontal cuticle and it surrounds a small calcified lamina, which grows into the hypostegal coelome. This coelomic expansion is in contact with the visceral coelome through the areolae and distal frontal septulae. Almost simultaneously, a second, crescentic lamina develops from the proximal part of the frontal shield of the next distal zooid. This, too, is surrounded by cuticle and by hypostegal coelome which is in contact with the visceral coelome of the distal zooid through its most proximal septulae. These are just visible, but are beginning to become sunk in calcification to form areolae. Like the avicularian subrostral chamber, this lamina appears to be a modification of the buttresses of calcification which alternate with the frontal septulae and grow upward into the hypostegal coelome (see pp. 109, 112). The second lamina thus grows upward into the expanded hypostegal coelome as a pair of crescentic, flattened buttresses, on either side of a thickened disc on the frontal shield. (When brood chambers are developed between two distal zooids, the second lamina can be seen to be derived from a buttress supplied by each zooid.) Concurrently, the shields of both maternal and distal zooids are becoming thicker, and their areolar buttresses are fusing to form interzooidal funnels. As the first lamina extends distally, the second grows distally and proximally, contacting the distal part of the maternal zooid shield and fusing with it. At this stage it therefore appears that the second lamina is derived from the maternal zooid (see Pl. 2A). The cuticle covering the laminae expands, so that they both grow outward into a 'bubble' of cuticle-covered, interzooidal hypostegal coelome. At this point, the cuticle covering the basal side of the first lamina, and that covering the frontal side of the second lamina may become isolated, and appear as a trace in longitudinal thin-sections. Both laminae extend laterally and distally and begin to curve frontally. They are closely apposed, but a minute space is visible between them (see Pl. 2F). Concurrent thickening of the distal zooid gives the developing brood chamber the appearance of being sunken in its frontal shield. There is still apparently some coelomic contact underneath the cuticle on the frontal side of the first lamina, as further thickening sometimes occurs on the surface at this stage (see Pl. 2E, F). The combined areolar funnels of the two zooids continue to lengthen as the frontal shields thicken, and these extend as tubes beneath the two laminae. The tubes open into the hypostegal coelome surrounding the brood chamber distally and laterally (see Pl. 2F).

At this stage the two laminae fuse, so that the minute coelomic space between them is 'pinched out'. In sections of complete brood chambers it appears to have become filled with calcification. The fused laminae continue to grow frontally and then curve medially, forming the raised, globular brood chamber. Secondary calcification also proceeds rapidly on the 'outer' side of the brood chamber. The change in microstructure is abrupt and can be seen in sections to be of the same form as that developed on the frontal shield of the zooids. As general, now extrazoooidal, thickening proceeds, the brood chambers become increasingly immersed but the funnels may remain visible (see Pls 1C, 6D). The brood chamber thus appears to be a type of highly modified, interzoooidal, frontal bud, derived from at least two zooids. It differs from the type of brood chamber found in *Bugula neritina*, which is a kenozooid derived from the zooid distal to the maternal zooid (see Woollacott & Zimmer, 1972), and from the type described in *Crassinarginatella* by Harmelin (1973 : 472), where the inner layer is part of the distal wall of the maternal zooid, and the outer layer is developed from the frontal wall of the distal zooid.

Some variation in sequences of development and their relative growth rates has been seen. In *T. celleporoides* the earliest stages appear at the growing edge, often at the earliest calcification of the frontal shield of the distal zooid. In *T. oranensis* and *T. mucronata* one to three zooids, and in *T. robusta* and *T. spatulata* two to four developing zooids, may intervene between the growing edge and the earliest recognizable sign of brood chamber growth. Variation in rates of growth

Table 1 Characters used in analysis.

Quantitative characters, as measured or counted					
1	Length of zooid				
2	Width of zooid				
3	Length of orifice				
4	Width of orifice				
5	Length of brood chamber				
6	Width of brood chamber				
7	Length of orifice of brooding zooid				
8	Width of orifice of brooding zooid				
9	Length of rostrum of interzoooidal avicularium				
10	Length of rostrum of vicarious avicularium				
11	Number of oral spines				
12	Minimum number of foramina				
13	Maximum number of foramina				
Qualitative characters		0	1	2	3
14	Form of colony		encrusting	unilaminar	bilaminar
15	Occlusion of frontal foramina		not occluded	occluded late in ontogeny	occluded early in ontogeny
16	Type of frontal thickening		general	funnels or blocks	
17	Suboral region	not thickened	thickened	macro present	
18	Orifice	no condyles or lateral indentations	indentations and/or condyles	large condyles, proximal sinus	
19	Types of avicularia	all absent	interzoooidal only	interzoooidal and vicarious	
20	Similarity of mandibles of two types	absent or only one type	similar	dissimilar	
21	Orientation of interzoooidal avicularia	absent	random to lateral	distinctly distal	
22	Shape of interzoooidal avicularian rostra	absent	expanded distally	rounded distally	acute distally

of parts of the brood chamber are illustrated by differences between those seen in *T. celleporoides* and in *T. mucronata* and *T. robusta*. In *T. mucronata*, the first lamina appears earlier and grows more rapidly than the second lamina. In some cases, calcification of the second lamina does not seem to occur and it appears as a cuticular cover, which does not calcify until later in ontogeny, when the secondary calcification is deposited. In some colonies of *T. robusta* the second lamina grows more rapidly than the first, and may even appear before it. The relative rates at which brood chambers develop may be roughly estimated among colonies by counting the number of zooid generations intervening between the earliest and the most complete stages in the development of the two laminae. In *T. perplexa*, *T. spathulata* and *T. oranensis* this may be as few as one to two generations; in *T. celleporoides*, *T. mucronata* and *T. robusta* development is less rapid and three to four generations may be present. Secondary calcification is also more advanced at an earlier stage in *T. spathulata*, *T. brancoensis* and *T. oranensis* than in the other species. The earliest astogenetic appearance of brood chambers may be correlated with the overall size of the colony. Species which have rather small, discrete colonies tend to produce brood chambers early; for example, they are present by the sixth zooid generation from the ancestrula in *T. perplexa* and *T. spathulata*. Other species with very large, erect colonies produce their brood chambers later in astogeny. Young colonies of *T. robusta* and *T. oranensis* comprising ten generations of zooids had no brood chambers.

Canu & Bassler (1923 : 168) stated that the 'ovicell' was 'endozoecial'. In a later paper (1928a : 43) it was described as 'hyperstomial and closed by the operculum', a description followed by several authors, e.g. Osburn (1950 : 98). However, the 'ovicell' of *T. sparsiporosa* (Canu & Bassler, 1928a : 50) was described as 'not closed by the operculum'. The relevance of the terms 'endozoecial' and 'hyperstomial' in the light of recent work on the ontogeny and structure of brood chambers is discussed briefly below (p. 124). The closure of the brood chamber by the operculum is one of the characters which may vary within a single colony in some Bryozoa; its state is also dependent upon the growth form of the colony and its preservation. In all specimens examined here the operculum, when present, is at a distinctly lower level than the opening of the brood chamber when in a closed position. When half open, it nearly closes the brood chamber opening, but the position in life during brooding is not known from direct observation. Later in ontogeny, brood chambers become immersed by calcification and this may give an impression that they are closed by the operculum. In the *T. spathulata*-group of species the space between the closed operculum and the roof of the brood chamber is proportionally less than it is in other species. In *T. musaica*, for example, some brood chambers appear to be closed by the operculum, others do not, but this seems to be a variation caused by difference in position at death and on preservation.

Coding of characters and results of polythetic clustering

In order to evaluate the degree of similarity among character correlations thirteen quantitative characters were measured or counted, and states of nine qualitative characters coded, for forty samples, see Tables 1 and 2.

Characters in *Tremogasterina* likely to be observable in many Recent and all fossil specimens are restricted to those preserved in the calcified skeleton. In living or well-preserved Recent material, many more characters are present which could be used for comparison among samples. Study of ultrastructure may also provide more characters than those at present recognized. Parts of colonies where zones of astogenetic repetition are present are comparable; zooids of overgrowth layers, which may be the only material available, sometimes show no more microenvironmental variation than those of primary layers, and are here regarded as comparable. Zooids of erect parts of colonies tend to vary less in overall dimensions than those of encrusting parts, which may be microenvironmentally affected. The ontogenetic state of zooids is more directly comparable, but the degree of ontogenetic thickening of the frontal shield may differ in its expression among species and sometimes among specimens of populations of species which have developed under different environmental conditions.

Table 2 List of forty samples analysed (see also Appendix, p. 140).

No.	Name	Reference	No.	Name	Reference
1	<i>T. problematica</i>	A. H. Cheetham	21	<i>T. robusta</i>	1975.10.4.1
2	<i>T. maçonnica</i>	A. H. Cheetham	22	<i>T. robusta</i>	1966.9.2.2
3	<i>T. areolata</i>	NMV	23	<i>T. aranensis</i>	1973.3.22.33
4	<i>T. pouyetae</i>	UCB	24	<i>T. aranensis</i>	1964.9.1.34A
5	' <i>T. miocenica</i> '	A. H. Cheetham	25	<i>T. aranensis</i>	1927.10.30.11
6	<i>T. lanceolata</i>	USNM	26	<i>T. brancoensis</i>	1964.9.1.43
7	<i>T. lanceolata</i>	1911.10.1.1713 1932.3.7.61	27	<i>T. brancoensis</i>	1973.3.22.35
8	<i>T. mucronata</i>	1911.10.1.1692	28	<i>T. brancoensis</i>	1964.9.1.38
9	<i>T. mucronata</i>	1965.8.2.1 1966.1.6.1	29	<i>T. celleporoides</i>	1961.10.30.11
10	<i>T. mucronata</i>	1911.10.1.1698	30	<i>T. celleporoides</i>	1944.1.8.272 1963.2.12.281
11	<i>T. mucronata</i>	1931.5.2.6	31	<i>T. celleporoides</i>	1962.2.20.7
12	<i>T. mucronata</i>	USNM 9766	32	<i>T. spathulata</i>	1961.10.30.9 1965.9.4.1
13	<i>T. mucronata</i>	USNM Fowey Light	33	<i>T. spathulata</i>	1971.3.16.1A
14	<i>T. mucronata</i>	USNM Alb. 2319	34	<i>T. spathulata</i>	1939.2.4.1
15	<i>T. subspatulata</i>	USNM Alb. 3005	35	<i>T. musaica</i>	1970.2.8.9pt
16	<i>T. subspatulata</i>	USC (<i>T. magnipora</i>)	36	<i>T. perplexa</i>	1973.3.22.27
17	<i>T. subspatulata</i>	USNM	37	<i>T. spathulata</i>	Midway Id
18	<i>T. subspatulata</i>	USC	38	<i>T. spathulata</i>	DG8 China Sea
19	<i>T. robusta</i>	1936.12.30.42	39	' <i>T. miocenica</i> '	Chipola Fm.
20	<i>T. robusta</i>	1965.2.4.11	40	<i>T. spathulata</i>	1975.9.24.4

Actual and relative rates of growth are unknown and there is thus no absolute time scale available for deciding which groups of zooids are strictly comparable. Generally, the measurements and other observations used here were taken from ten zooids from a zone of repetition which did not show any microenvironmental influences such as crowding, etc. In the case of some Recent specimens, and practically all fossil colonies, no such exact conditions could be applied. Preservation of both fossil and Recent material also alters characters and makes some observations difficult. The characters and character states used here are given in Table 1, and the details of specimens coded in Table 2. Data, nearest neighbour and coordinate tabulations are stored at the British Museum (Natural History).

The following notes describe some of the characters used:

CHARACTERS 1 AND 2. During ontogenetic thickening of calcified walls, the limiting vertical walls of zooids become completely obscured (see p. 107). The length and width of zooids has therefore been measured from the distalmost edge of the orifice of one zooid to that of the next in direct distal sequence. Where even the edges of orifices were obscured or worn, the mid-point of common funnels in the calcification between zooids has been used as a demarcation in measuring both length and width of zooids.

CHARACTERS 3, 4, 7, 8 AND 18. As the frontal shield thickens, the orifice appears to become larger in some specimens, and its shape becomes less regular. Wherever possible, measurements have therefore been made at the earliest ontogenetic stage after completion of the orifice and condyles. The very nature and relatively late ontogenetic development of the umbonuloid secondary orifice make it more susceptible to microenvironmental influences than the primary calcified orifice of its cryptocystidean counterpart. There may be a great deal of variation within a colony in orifice size and shape (see Pl. 5C), and in some species there is a slight but significant difference in the means and range of the orifice dimensions in brooding zooids. Condyle and 'sinus' development can be seen in all but very worn specimens.

CHARACTERS 5 AND 6. Brood chambers are frequently influenced by development of surrounding zooids. In addition, secondary thickening may radically alter measurements.

CHARACTERS 12, 13, 15 AND 16. The number of foramina is greatly influenced by ontogeny, but does seem to have some 'specific' correlations in range, if not in absolute number. Foramina may be subdivided or obscured during ontogeny, or surrounded singly or in groups by funnels and blocks of calcification; they are also susceptible to wear. The extent and type of frontal shield thickening does seem, within fairly wide limits, to be genetically controlled.

CHARACTERS 9, 10, 19, 20, 21 AND 22. Avicularian rostra are often much affected by wear in fossil specimens. Their orientation and rough dimensions are usually observable, and although the distal part of the rostrum is somewhat vulnerable, it is often well-preserved enough for its shape to be inferred in one or two examples in a colony. Variation in mandible shape among colonies of a species or population is common, variation within a colony occurs more rarely.

The results of clustering have shown that overall morphological similarity broadly parallels the groupings, and also indicates the apparent evolutionary trends, which were concluded from inspection. 'Anomalies' in cluster formation are interesting because they indicate the relative importance of some 'characters'. They also reveal possible inadequacies in the input of original data, and they illustrate the very close morphological similarity among some populations widely separated in space and time.

Of the ten clusters of samples which separated in three dimensions (see Fig. 5), only two, *T. lanceolata* (6 and 7) and *T. celleporoides* (29-31), were completely inclusive of samples nominally assigned to the species, and exclusive of any other sample. The cluster of *T. oranensis* samples (23-25) included one of *T. brancoensis* (27), which is not surprising, in view of the close morphological similarity of some, but not all, populations of these two species (see p. 134). The samples of

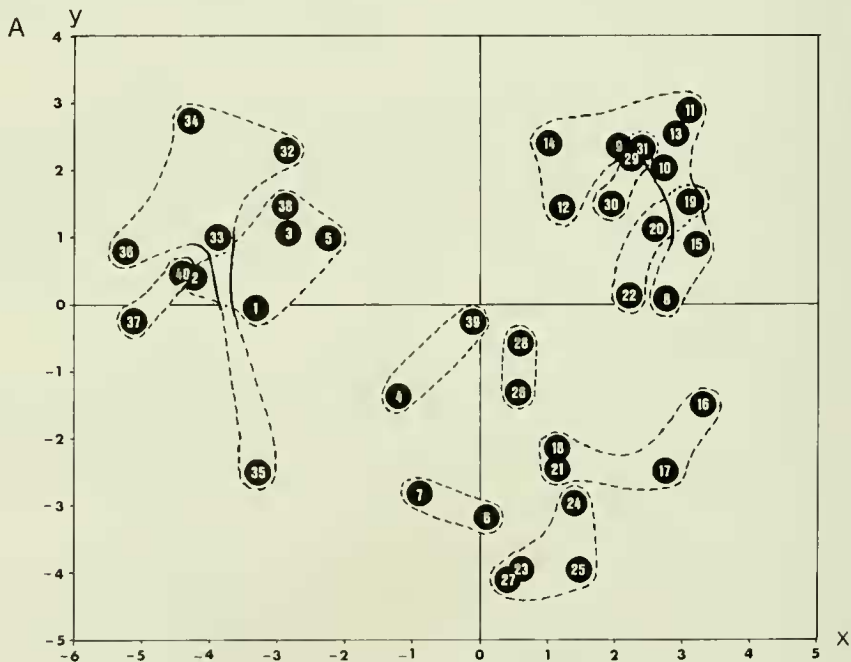


Fig. 5A Ordination diagram, prepared by the principal coordinate algorithm (see Gower, 1966). Squared distance in proportion to (100 - similarity). See Table 2 for key to numbering; data and coordinates stored at BMNH. Coordinates X, Y. Note separation of three clusters of 'fossil' and *T. spatulata* samples (1-3, 5, 32-38, 40) from remaining clusters.

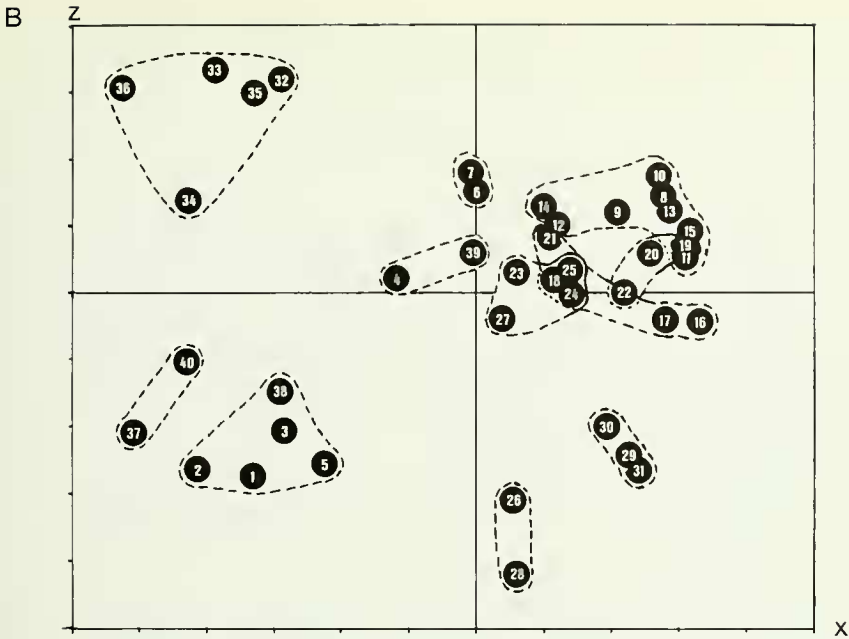


Fig. 5B Ordination diagram, as Fig. 5A. Coordinates X, Z. Note consistency of separation as in Fig. 5A, and in close association of *T. robusta* (19, 20, 22) and *T. mucronata* (8-14) clusters.

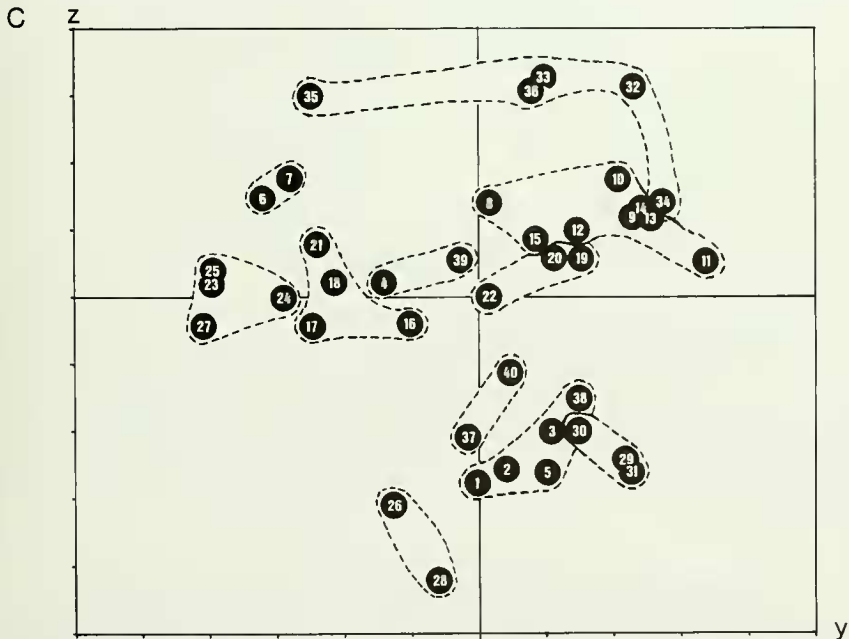


Fig. 5C Ordination diagram, as Fig. 5A. Coordinates Y, Z. Note consistent separation of small clusters (4, 39), (6, 7), (16-18, 21), (23-25, 27), (26-28) and (29-31).

T. mucronata from the Gulf of Mexico (8–14) clustered closely together, but included one sample of *T. subspatulata* (15). This cluster was well separated from that of the remaining Californian samples of *T. subspatulata* (16–18) which, however, included the ? Pleistocene sample of *T. robusta* from the Red Sea (21). The characters of these last two species are very similar, particularly in the size, shape and orientation of the avicularia and occlusion of frontal foramina. The deciding factor in the 'anomalous' position of the Red Sea sample appear to have been connected with zooidal size characters. The zooids of the ? Pleistocene sample are significantly smaller than those of other, Recent *T. robusta* specimens (see p. 134). These *T. robusta* samples (19, 20, 22) showed a very close association with the *T. mucronata*-cluster in three dimensions. Nearly all the 'fossil' samples (1, 2, 3, 5) clustered together, and included one sample of *T. spathulata* (38). Three of the remaining *T. spathulata* samples (32–34) formed a diffuse but distinct cluster with *T. perplexa* (36) and *T. musaica* (35). Exceptions to these two groups were *T. pouyetae* (4) and one sample of '*T. miocenica*' (39), and two samples of *T. spathulata* (37, 40) which formed two distinct clusters. Generally, these closely involved clusters of fossil and *T. spathulata* samples were well separated from all other samples as a sub-group. Here again, zooidal size characters appear to have been a deciding factor. The close morphological similarity between, for example, the sample of Recent *T. spathulata* (40) from the Seychelles and the Eocene *T. maçonica* is, however, noted on p. 137 (see also Pl. 5A and Fig. 8A).

In order to test possible weighting by a preponderance of 'avicularian' and 'foramen' characters, and to test the relationships within the two major subgroups of clusters, three characters (Nos 13, 19, 20) were discarded and the *T. mucronata*-*subspatulata*-*lanceolata* samples were isolated and re-clustered, as were the 'fossil' and *T. spathulata* samples. In both cases, relationships within and among groups remained virtually unchanged.

The clusters illustrated in the ordination diagrams (Figs 5A, B, C) were constructed from the values for nearest neighbour pairs. Generally, percentage similarities among the samples was not very high. Among the highest was a value of 96% between *T. celleporoides* (29 and 31), 95% between *T. lanceolata* (6 and 7) and 93% between *T. subspatulata* (16 and 17), *T. mucronata* (9 and 10) and *T. oranensis* (23 and 25). Examination of the values for second nearest neighbour pairs emphasized the close similarity between other pairs of samples. For example, the 'anomalous' sample of *T. subspatulata* (15) had an 86% similarity with *T. mucronata* (13) but a very close, secondary similarity of 85% with *T. subspatulata* (16). The *T. oranensis* sample from Angola (23) had a 93% similarity with the sample from Cap Blanc (25) but an 89% secondary similarity with the Angolan sample of *T. brancoensis* (27). Similarly, although the 'anomalous' samples of *T. spathulata* (37, 40) had an 88% similarity with one another, the second nearest neighbour in both cases was the fossil *T. problematica*, at 84%, parallel with the 86% similarity between *T. problematica* and the *T. spathulata* sample from the South China Sea (38).

As mentioned above (p. 116), the number and nature of the characters available in comparison of fossil with Recent specimens is restricted, but it has become evident that all the characters used at present to distinguish species within *Tremogasterina* populations rely heavily upon isolation in time and space. Relationships among both the fossil and Recent representatives of the *T. mucronata*-complex, and among the *T. spathulata* samples, are examples of the difficulties inherent in assessing a fairly large number of individual samples, none of which is really complete enough to establish limits of intra-sample astogenetic and ontogenetic variation. Both intra- and inter-specific variation and morphological similarities are pronounced within *Tremogasterina*; the samples are, however, separable in time and space. Although some of the criteria used here to divide populations are arbitrary and possibly not consistently applied, the groupings attained both by clustering and by inspection have been used here as the basis of the tentative evolutionary series given below.

Evolutionary trends and distribution in time and space

In the absence of large and widely distributed populations of fossil specimens, any attempt to reconstruct the evolutionary history of the genus can be only of the most tentative kind. There are indications, however, that two major, divergent trends in morphological change may have occurred.

The first was towards increase in the number of frontal foramina, while retaining the characters of encrusting habit and small zooid and avicularium size typical of the earliest known fossil specimens. This resulted in the Recent forms like *T. spathulata*, *T. perplexa* and *T. musaica*. The second trend was towards a reduction in the number and extent of frontal foramina, ending in their occlusion early in ontogeny. This was accompanied by considerable development of extra-zooidal tissue, allowing the potential for an erect habit, and was accompanied in some forms by an increase in the size of the zooids and the avicularia, which last became more regularly distal in orientation. This resulted in the Recent forms like *T. mucronata*, *T. lanceolata*, *T. robusta* and *T. oranensis*.

The Eocene species, *T. maçonica*, is of great interest in that it combines some of the characters of both these trends. The small zooids are encrusting, and the foramina have distinct rims of calcification in some cases, similar to the early stages of the formation of blocks of calcification seen in the *T. spathulata*-group. At the same time, the number of foramina is far lower, and the orifice has the rounded, non-sinuate shape found in later populations of *T. mucronata*. The orifice in *T. maçonica* also resembles that of some cribrimorphs and *Arachnopusia* in appearance. There is a distinct, raised, proximal apertural bar, and the distal part of the orifice slopes in a basal direction away from this level. Similar orificial characters are present in the primary distal zooids budded from the ancestrulae of several Recent species (see Fig. 1), which suggests that this may be a 'primitive' character state. Elongation of the orifice, and the appearance of a proximal 'sinus', occurs in the Miocene *T. pouyetae*, but reaches its greatest development in both the *T. spathulata* group (in *T. musaica*), and in the *T. mucronata-lanceolata-robusta* group (in *T. oranensis*).

Umbonuloid species do not seem to form multilaminar or erect colonies by colony-wide frontal budding, as do many cryptocystidean forms. Frontal budding occurs sporadically, and is followed by overgrowth layers. Cheetham (1971) has analysed the correlation of methods of thickening and strengthening the frontal wall in cheilostomes with the evolution of the erect habit. Most Recent species of *Tremogasterina* have encrusting, multilaminar colonies, which rise into unilaminar, often tubular, erect expansions. These are often thickened by overgrowth layers. The same form of growth occurs in *T. oranensis*, but *T. brancoensis* is truly bilaminar, although here too, the erect branches are later strengthened areas by of overgrowth.

It is inferred here that the descendants of the earliest Atlantic populations (*T. problematica*, *T. maçonica*) gave rise to the Miocene populations represented on the one hand by '*T. miocenica*' and *T. mucronata* in North America and the Gulf-Floridan region, and on the other hand by *T. areolata* and *T. pouyetae* in southern Europe. The wide Recent distribution and intraspecific diversity of populations of *T. spathulata*, coupled with the one Pliocene record from Midway Is., suggest that it, too, may have been derived from an extensively distributed, *T. maçonica*-like form. The possibility that the Recent west African *T. perplexa* and *T. musaica* are similarly derived is purely speculative. The similarities in zooidal and orificial characters among the Miocene *T. areolata* and *T. pouyetae* and the ? Pleistocene-to-Recent *T. robusta* populations indicate that they may be related. If so, this *T. robusta* group is a further example of the migration (or more probably of the progressive restriction) of shallow-water, southern European Miocene forms to the Indo-Pacific region (see Lagaij & Cook, 1973). *T. robusta* also has features in common with the *T. oranensis-T. brancoensis*-complex, but the absence of African fossil specimens precludes any inferences as to the closeness of this relationship. Without fossil evidence it is also impossible to suggest a derivation for the Recent western Pacific populations of *T. celleporoides*. There is apparently no Tertiary record of *Tremogasterina* from Australia (see p. 123), and generally, the characters of *T. celleporoides* have more in common with those of *T. mucronata* than with those of *T. robusta*, although it seems unlikely that it could have been derived from the American species complex.

Geographically, the Recent forms fall into three distributional groups (see Maps 1, 2, pp. 145, 146). In the Indo-Pacific (*T. spathulata*, *T. robusta*, *T. celleporoides*), *T. spathulata* has the most extensive, and *T. celleporoides* the most restricted range. In the eastern Atlantic (*T. oranensis*, *T. brancoensis*, *T. perplexa* and *T. musaica*), the first two species have a wide range and form an interesting complex which may show either divergence or convergence of characters (see p. 135).

T. perplexa and *T. musaica* are as yet known from few records, but probably have a larger range in this area. The third group of populations extends through a large area from Florida and the Gulf of Mexico, the Caribbean and Brazil, to California, western Mexico and Panama. The populations are here grouped together as three species-groups (*T. lanceolata*, *T. mucronata*-complex and *T. subspatulata*). It is interesting that whereas very similar species included in the *T. spathulata*-group are present in the eastern Atlantic and Indo-Pacific, there is apparently no Recent record of any similar form from the western Atlantic or eastern Pacific region. An Oligocene form, *Arachnopusia vicksburgica*, was however described from the Vicksburgian of Mississippi by Canu & Bassler (1920 : 311, pl. 85, figs. 1-3) The colonies were rare; they encrusted shells, and had large zooids (Lz 0.65-0.72 mm), with ten to fifteen frontal foramina, each surrounded by a polygonal area of calcification. No oral spines were mentioned, and the 'hyperstomial' brood chambers were covered by calcification which in the retouched figures resembles the blocks of secondary tissue found in *T. musaica*. Small, rounded, interzooidal avicularia were present. It is possible that *A. vicksburgica* is related to the *T. spathulata*-group of species, but it requires further investigation.

Many of the species, both fossil and Recent, are associated with oyster shells, although coral is also a frequent substratum. *Tremogasterina* typically extends into shallow water, but the distribution of several species descends into deep water, and *T. robusta* is the only form confined to depths of less than 37 metres (see Powell, 1967 : 166). The known depth ranges are given in Table 3.

Table 3 Depth ranges of *Tremogasterina* spp.

Species	Depth range in metres	Species	Depth range in metres
<i>T. robusta</i>	0-37	<i>T. subspatulata</i>	9-104
<i>T. musaica</i>	50	<i>T. lanceolata</i>	146-271
<i>T. perplexa</i>	50	<i>T. celleporoides</i>	0-420
<i>T. brancoensis</i>	50-73	<i>T. spathulata</i>	0-430
<i>T. oranensis</i>	20-100	<i>T. mucronata</i>	60-506

Relationships among umbonuloid cheilostomes

The sequence of changes in the ontogeny of the frontal shield in *Tremogasterina* resembles both that in *Tripurula* and *Exechonella* (see Cook, 1967) and that in *Adeona* (see Cook, 1973). These three genera differ from *Tremogasterina* in the absence of oral spines and external brood chambers.

Some of the species here assigned to *Tremogasterina* have been previously placed in *Hiantopora* and *Arachnopusia*. The characters and limits of these two genera need investigation and revision. Generally, *Hiantopora* differs from *Tremogasterina* in that the frontal shield develops asymmetrically and unilaterally. It is composed of anastomosing spinous processes which are calcified both frontally and basally, with an intervening coelomic space. Development in *Arachnopusia* is very similar to that in *Tremogasterina*. The calcified frontal shield is umbonuloid and consists of branching and anastomosing processes. The frontal septulae are minute but do not extend distally round the secondary calcified orifice. The sequence of developmental episodes in the oral region differs from those in *Tremogasterina*. Zooids at the growing edge show that the oral spines, which often develop unilaterally, are differentiated before the delineation of the secondary calcified orifice is complete. The brood chambers, too, are well developed at this stage. In *Tremogasterina* brood chambers may develop early in ontogeny, but not before the partial completion, at least, of the frontal calcified shield of the next distal zooid.

Hiantopora liversidgei Tenison Woods (1876 : 149) resembles *Tremogasterina* in possessing one to three large, reniform frontal foramina. Specimens in the British Museum (Balcombe Bay, Victoria, Miocene D35451) show what appears to be a unilateral spine base preserved in some zooids. The brood chambers and adventitious avicularia are very similar to those found in species

assigned to *Arachnopusia*, and this is almost certainly where its affinities lie (see Brown, 1952 : 178). Waters (1881 : 328) described *A. liversidgei* as '*Mucronella mucronata* Smitt', this suggesting that it was identical with the Recent Floridan species belonging to *Tremogasterina*. At present, no Tertiary form of *Tremogasterina* is known from the Australasian region.

As noted below (pp. 135, 136), two of the species here included in *Tremogasterina* were originally assigned to *Lepralia*, and later considered to belong to the cryptocystidean ascophoran genus, *Cleidochasma* Harmer (see Cook, 1964 : 11). There is increasing evidence of parallel series of genera, with species which have many similar characters, but which seem to have evolved convergently. These genera have alternatively either umbonuloid or cryptocystidean frontal shield ontogeny. This distinction is not a monothetic one, but involves many character correlations of body wall layers, ontogenetic sequences and orificial relationships.

In addition to the *Adeona*-*Adeonella* and *Tremogasterina*-*Cleidochasma* series, recent investigations have shown that among the overwhelmingly cryptocystidean 'smittinid' genera, there are also forms which have umbonuloid development. The 'smittinid' genera include a wide diversity of forms (see Osburn, 1952; Ryland, 1963; Soule & Soule, 1973), but have a single character in common. This is the presence of a well-developed proximal oral denticle (lyrula). The species described by Powell (1968 : 2303, pl. 9, fig. d) as *Escharella thompsoni* Kluge is represented in the British Museum collections by specimens from southern Greenland (Nanortilik, 110 metres, 1969.3.24.19-22), which have well-preserved growing edges showing complete ontogenetic series of umbonuloid development. The type-species of *Escharella*, *E. immersa* (see Ryland, 1963 : 18), is cryptocystidean. Similarly, the species described by Calvet (1909 : 32, pl. 3, fig. 7) as ? *Phylactella lyrulata* is represented in the British Museum Collections by specimens from the Antarctic (McMurdo Sound, 45-366 metres, 1967.2.8.136, 138 and eastern edge of ice barrier, 162°30' W, 182 metres, 1967.2.8.137) which, unlike the type-species of *Phylactella*, *P. labrosa* (see Ryland, 1963 : 18), have umbonuloid frontal shield development. In both these forms the basal part of the umbonuloid fold advances as a continuous sheet of calcified tissue. The completed frontal shield has no foramina, but there is peripheral series of areolae derived from frontal septulae alternating with raised buttresses, very similar to that illustrated by Cheetham (1968, pl. 10, fig. 3) in the umbonuloid genus *Metrarabdotos*. This form of shield is also found in specimens of *Coleopora seriata* Canu & Bassler (1929, BMNH, 1931.12.38.87) and in the specimens from Borneo (BMNH, 1851.1.20.11), described as *Teuchopora* sp. by Harmer (1957 : 898, text-fig. 97). Other specimens of *Coleopora*, such as those described by Harmer (1957 : 898) as *Teuchopora verrucosa* (Canu & Bassler, 1929), which are part of Canu & Bassler's material of *C. verrucosa* from the Philippines (BMNH, 1931.12.30.85), have an umbonuloid frontal shield development with foramina similar to that of *Exechonella*. Thus, even within one nominal generic grouping of umbonuloid species there are differences in frontal shield ontogeny which may indicate that in spite of general similarities in colony form and zooid appearance, there may be little systematic relationship among the specimens.

Problems arising and further fields of work

Apart from the nomenclatural problems inherent in the descriptions of the type and other species (see p. 125), study of *Tremogasterina* has revealed several aspects of morphology and distribution which require further work.

One of the principal problems in current cheilostome systematics is the establishment of correlations between structures associated with the ontogeny of the calcified frontal shield and the hydrostatic apparatus, which would be recognizable in fossil specimens. Some preliminary correlations which allow tentative inferences have been noted by Cheetham (1968), Banta (1971) and Cook (1973). The umbonuloid ontogeny and basically anasciform affinities of some of the species now assigned to *Tremogasterina* were not recognized until complete ontogenetic series were available. It is possible to infer umbonuloid ontogeny from isolated episodes and from a correlation of characters such as frontal septulae and the form of the secondary calcified orifice (see also Cook, 1973). The nature of the ontogenetic sequences and the homology of the layers involved are not always observable in fossil or Recent material in an advanced state of calcifica-

tion. At present, there are few criteria available allowing inferences on ontogeny to be made from such specimens. The confluent nature of the hypostegal coelomes perhaps allows only the generalization that at any point above frontal septula, some form of interzooidal frontally budded structure is possible. The presence of a hypostegal coelome itself may be inferred in specimens without 'soft parts' from the coalescence of areolae and eventual colony-wide extrazooidal calcification. It is probable that specimens of fossil forms exist in which the frontal foramina are occluded, and the orifice is elongated, with large condyles and a proximal sinus, like *T. oranensis*. Conversely, species like *T. spathulata*, with a large number of foramina surrounded by blocks of calcification, may be found as fossils in the future. Their recognition as forms belonging to *Tremogasterina* may depend entirely upon the presence of a series of zooids showing the frontal shield ontogeny. Large gaps are also present in the known geographical distribution and fossil record. A range of Eocene to Pliocene specimens from western Africa, southern Europe and the Indian Ocean at least would be necessary to trace the history of the many Recent forms. Now that some of their characters have been recognized, it is possible that the affinities of some of these forms may be traced in the future. Further examination of both Recent and fossil oyster and coral faunas for encrusting Bryozoa would be one of the first steps in the search for specimens showing morphological states linking known forms in time and space.

Work on microstructure and ultrastructure of the calcified walls may yield characters and character states which can be correlated with known ontogenetic sequences. Preparation of thin-sections of hard and soft parts of known relationship *in situ* is the first step in discovering such correlations.

The tracing of the ontogeny of the brood chambers from Recent, well-preserved material raises the problem of terminology of such structures in less complete fossil and Recent material. The terms 'hyperstomial' and 'endozoecial', for example, derive from the concept that the brood chamber is necessarily 'part of' the proximal zooid, i.e. the zooid which produces the ovum which is to be brooded. Recent work by Woollacott & Zimmer (1972) has confirmed that some brood chambers are in fact kenozooids derived from the zooid *distal* to that which produces the ovum, and in communication with the distal zooid through septulae. Harmelin (1973) has also shown that an apparently 'hyperstomial ovicell' may be constructed of elements derived from both the maternal zooid and from the distal zooid, and that the brood chamber cavity is basically 'within' the distal zooid and thus 'endozoecial'. It seems that until many more ontogenetic series have been described, general terms which infer zooid relationships should be used with caution, and when used should carry with them the connotation that developmental series were not available for observation in the material described.

Other problems in recognition of structures of differing ontogeny, but similar appearance at full development, are involved in the description of communication pores. As noted above (p. 110), it would appear that pores with chambers may be part of a continuum of structures, and the terms 'diatella' or 'pore chamber' should also be used with caution.

However convenient all such terms may be in describing a structure, they do tend to obscure investigation of the actual developmental relationships concerned.

A study of variation both within and among populations should be made, using more plentiful material with more ecological data than that so far available. More characters would arise for comparisons, and in conjunction with studies of fossil specimens might lead to a reconstruction of the systematic relationships and evolutionary trends which would approach more closely to the real relationships and ecology of the group than that inferred here.

Systematic section

The genera *Poricella* and *Tremogasterina*

Both genera were originally erected by Canu; *Poricella* for *P. maçonica* (Canu, 1904 : 28, pl. 35, fig. 43, from the Eocene of southern Tunisia), and *Tremogasterina* for *T. problematica* (Canu, 1911 : 256, pl. 7, figs 12, 13, from the Paleocene of Argentina, see p. 127).

These two species are considered here to be congeneric, and therefore it would appear that *Tremogasterina* is a junior subjective synonym of *Poricella*. However, the descriptions and characters of the type-species of both genera pose several problems of interpretation and nomenclature, and complete elucidation requires detailed examination of the type-specimens, and of other specimens involved. It is therefore not proposed here to introduce any formal designations, but to summarize briefly the history of the two genera and to indicate the problems arising.

Poricella was defined by Canu (1904 : 28) in the following terms: 'Zoécies convexes, perforées de plusieurs micropores. Apertura semi-lunaires. Génésies de même forme que les autres zoécies, mais de dimensions plus grandes et perforées par un plus grand nombre de pores. Avicellaires intercalés. Lutétien, Actuelle. Affinités. Ce genre comprend les trois sortes de zoécies qui caractérisent la famille des Adéonées de Busk. Ses perforation dorsales le rapprochent des Hiantoporidées de MacGillivray, mais elles n'ont peut-être pas la même fonction.'

The designated type-species, *P. maçonnicca*, an Eocene fossil, was the only species assigned to the genus. No Recent ('actuelle') species or specimens were described, and as *P. maçonnicca* was encrusting, no basal ('dorsale') perforations were mentioned. The description of *P. maçonnicca* included the remarks: 'Perforations frontales au nombre de trois, en triangle sur les zoécies ordinaires et plus nombreuses sur les génésies. Génésies de dimensions plus grandes. Avicellaires intercalés, plus petits que les zoécies, assez rares.'

The term 'génésies' was used consistently by Canu for enlarged, dimorphic zooids with internal ovisacs, as found in the Adeonidae. The term he used for external, calcified brood chambers was 'ovicelles'. The figure of *P. maçonnicca* (Canu, 1904; pl. 35, fig. 43) has been retouched, but shows approximately twelve zooids clearly. Two zooids have broken, but distinct 'hyperstomial ovicells', and none of the zooids is obviously dimorphic in any way, nor do any of them have more than three frontal pores. Photographs of the type-specimens of *P. maçonnicca*, kindly supplied by Dr A. H. Cheetham, show zooids and numerous brood chambers very like the 'ovicells' in Canu's figure (see Pl. 3C, D).

In the section on the affinities of *P. maçonnicca* Canu remarked 'J'ai trouvé dans le bassin de Paris une espèce très voisine qui n'est pas encore décrite.' It is possible that part of his generic definition and even of his description of *P. maçonnicca* was based on specimens of this species, which had 'génésies', but which was not in fact formally described until several years later. In a subsequent paper on fossil species from Paris, Canu¹ (1907 : 150 (sep. p. 46), pl. 6, figs 5-8, text-fig. 3) introduced *Poricella elongata* from the Ypresian and Lutetian, and included *Mucronella sutneri* Koschinsky in *Poricella* (Canu 1907 : 47, pl. 9, fig. 1, text-figs 4, 5). Canu's (1907) figures of *P. elongata* are of a typically 'adeonid' species, and one (fig. 8) specifically shows the 'génésies'; large dimorphic brooding zooids. Koschinsky (1885 : 57, pl. 3, fig. 9) had given an excellent figure of *M. sutneri*, showing that it too, is an 'adenoid' species.

The concept of *Poricella* as a genus possessing dimorphic brooding zooids, in spite of the characteristic 'ovicells' present in the type-species, was emphasized by Canu in 1907, in his discussion of the genus. He remarked 'J'ai créé ce genre en 1904 pour une espèce du Tertiaire de Tunisie, mais en ajoutant que certaines espèces fossiles et actuelles pouvaient y être introduites. M. Waters me fit alors constater' (presumably in a personal communication) 'que ce genre faisait double emploi avec *Hiantopora* MacGillivray. Malgré des analogies évidentes, je crois cependant devoir maintenir le genre *Poricella* qui diffère de l'autre par la présence de génésies, c'est-à-dire, de deux sortes de zoécies à fonctions distinctes comme dans toutes les Adéonées de Busk.' Waters (1912 : 497) appears to have eventually accepted this statement, as he remarked 'There are gonocœcia' (i.e. 'génésies') 'in the fossil *Poricella* Canu.' Subsequent records of *Poricella*, for example that of *P. davidi* Balavoine (1960 : 248, pl. 7a, fig. 5), are also of 'adeonid' species.

The further history of *Poricella* has extended the confusion. Canu & Bassler (1920 : 558, fig. 166N), included copies of Canu's text-figure of 1907 of *P. elongata*, when illustrating the characters of another adeonid genus, *Bracebridgia*. They did not, however, include either *P. elongata* or *P. sutneri* in the list of species they attributed to the genus (p. 567). In the same paper (p. 564) they included *Poricella*, with other genera 'which may be admitted as artificial subgenera in order to

¹ For dating and pagination of the various parts of Canu (1907-1910), see Reference section.

facilitate classification' in *Adeonellopsis*, and listed *P. maconnica* as belonging to that genus. Canu & Bassler (1928a : 44-45) included *P. maconnica* in *Tremogasterina* (see below), but Bassler (1935 : 174 and 1953 : G213) continued to regard *Poricella*, with its type-species *P. maconnica*, as 'a synonym or subgenus of *Adeonellopsis*'.

Examination of type and other specimens may show that some or all adeonid species presently assigned to *Poricella* could be placed in *Adeona* or *Adeonellopsis*. If any of them are distinct, however, it will be necessary to erect a new genus to accommodate them.

Tremogasterina was defined by Canu (1911 : 256) in the following terms: 'Frontale perforée par une grande ouverture qui en occupe presque toute la surface.' *T. problematica* was described with a frontal foramen larger than the orifice, which was wider than long. Small elliptical or fusiform interzooidal avicularia were present, with paired condyles. The ovicell was subglobular, not prominent, and opened into the interior to the zooid. Unfortunately, the zooids figured by Canu (1911; pl. 7, figs 12, 13) are practically unrecognizable. The photographs show fairly regularly arranged zooids, with small, randomly orientated avicularia. The specimen was obviously very worn and little more of its characters can be seen. Some specimens of a species of *Tremogasterina* are now known from the type-locality of *T. problematica*, they are discussed below (p. 127).

The nature of the brood chambers in *Tremogasterina* continued to be obscure. Canu & Bassler (1923 : 168, pl. 24, figs 3, 4) described *T. horrida* from the Miocene of Florida with 'endozoecial ovicells', and stated that 'the ovicell is concealed' in their description of the genus. Their specimens did not have ovicells 'in a condition to be photographed', but in the same paper they described '*Cribrilina cuspidata*' from the Miocene of Cuba (p. 88, pl. 15, fig. 16) with 'hyperstomial ovicells' and noted that it was 'very little distinct from *Escharipora mucronata* Smitt'. They seem to have overlooked the very obvious similarities between the two Miocene species at this time, but in their later paper on the fauna of the Gulf of Mexico (1928a : 43-44), they gave *T. problematica* Canu, *P. maconnica* Canu, *E. mucronata* Smitt and *L. areolata* Reuss, together with *T. horrida* and *C. cuspidata* in a list of species included in the genus *Tremogasterina*. All these forms are considered here to belong to *Tremogasterina*, but one species included by Canu & Bassler (1928a), '(*Galeopsis*) *convexus* Canu & Bassler 1920', does not appear to belong to the genus.

TREMOGASTERINA Canu, 1911

Type-species *T. problematica* Canu.

The character correlations defining *Tremogasterina* as used here are as follows. Colony encrusting and erect, with secondary overgrowths of zooids arising from frontal buds. Ancestrula membraniporiform. Zooids with umbonuloid development of the frontal shield, developing from a curved lamina which forms a secondary calcified orifice and large proximal foramen by anastomosis of paired lateral processes. Secondary calcified orifice large, with lateral indentations and frequently with lateral condyles. Oral spines present, oral shelf slight or absent. Frontal foramina often subdivided, remaining open or uncalcified in some forms, becoming occluded at various stages in the ontogeny of others. Secondary thickening of the frontal shield usual, sometimes resulting in the development of a suboral micro and/or calcified ridges. Zooids communicating by distal and lateral multiporous septulae, which become surrounded by deep, calcified buttresses during ontogeny, sometimes forming chambers similar in appearance to diatellae. Zooids with a row of frontal, marginal multiporous septulae, which frequently extend distally completely round the orifice. Frontal septulae becoming obscured in late ontogeny, or surrounded by buttresses of calcification, eventually coalescing to form interzooidal funnels. Avicularia interzooidal, arising from frontal septulae of adjacent zooids; vicarious avicularia often also present. Mandibles hinged on a complete bar or on long, spinous, paired processes. Brood chambers arising as modified interzooidal frontal buds from the frontal septulae of sequential zooids, prominent at first ('hyperstomial'), becoming immersed by secondary calcification, not closed by the operculum.

REMARKS. Species are included in which the frontal foramina are present only at the earliest ontogenetic stages, and become occluded during ontogeny. Although fossil colonies here attributed

to *Tremogasterina* are fairly plentiful, they have been recognized only as forms with open frontal foramina. Complete occlusion of the foramina results in such a different appearance that relationships can only be traced where ontogenetic series are available, as in the Recent species *T. oranensis* and *T. brancoensis*. Consequently, it is possible that fossil forms with occluded foramina occur, but have not yet been recognized as belonging to *Tremogasterina*.

Tremogasterina problematica Canu

Tremogasterina problematica Canu, 1911 : 256, pl. 7, figs 12, 13, Rocanéen de Roca, Argentina, Paleocene (see below).

MATERIAL EXAMINED. Photographs of *Tremogasterina* sp. from the type-locality of *T. problematica* (see below).

DESCRIPTION (Pl. 3A, B). This description is based on that of Canu (1911) together with observations based on photographs of a species of *Tremogasterina* kindly supplied by Dr A. H. Cheetham. Colony encrusting, frequently on oyster shell. Zooids with a flat frontal shield rising distally to a thickened bar proximal to the orifice. Orifice rounded distally, straight proximally, with no obvious mucro or condyles. Two distal oral spines present in brooding zooids. Frontal shield with one to five foramina. Funnels present between zooids, and chambered septulae present. Avicularia interzooidal, subrostral chambers not much raised, placed near zooid orifices and oval in shape, orientated randomly. No bar or condyles seen. Brood chambers not very prominent, imperforate frontally.

MEASUREMENTS (in mm).

Lz 0.42-0.50 Lo 0.11-0.14 Lov 0.18-0.19 Lr 0.07-0.10
lz 0.20-0.30 lo 0.11-0.13 lov 0.18-0.21

REMARKS. Canu gave the age of the Roca formation as Cretaceous. Buge (1946) has discussed the age of some of the Argentinian formations from which specimens were described by Canu in 1908, but not those described in 1911. Bertels (1969) gave the age of the Roca formation as Paleocene (Lower Danian). Dr A. H. Cheetham (*pers. comm.*, 1975) has informed me that 'according to Dr Bertels (*pers. comm.*, 1969) the type-locality for the Bryozoa described by Canu is Barranca del Jaguél, Neuquén Province'. Dr Cheetham has examined a sample of material from this area, and has found the specimens of *Tremogasterina* sp. figured here on Pl. 3A, B. Canu's figures (1911 : pl. 7, figs 12, 13) are of a specimen so worn as to be practically unrecognizable, but if it does belong to *Tremogasterina* as defined here, it appears almost certain that the specimens examined by Dr Cheetham are of *T. problematica*.

Tremogasterina maçonica (Canu)

Poricella maçonica Canu, 1904 : 28, pl. 35, fig. 43, Tunisia, Eocene.

Tremogasterina maçonica Canu, see Canu & Bassler, 1928a : 44.

MATERIAL EXAMINED. Photographs of the type-specimen of *T. maçonica*.

DESCRIPTION (Pl. 3C, D). Colony encrusting oyster shell, with overgrowth layers. Zooids small, with rounded frontal shields. Orifice with lateral indentations and a small proximal mucro on a distinct, thickened suboral bar. Three to four frontal foramina, rounded or lunate, sometimes occluded, with distinct rims and suture lines. A few interzooidal funnels present, little general thickening. Avicularia numerous, small, with rounded rostra and a bar, orientated randomly. Brood chambers (all broken) 'hyperstomial'.

MEASUREMENTS (in mm).

Lz 0.30-0.33 Lo 0.07-0.10 Lov 0.12-0.14 Lr 0.06-0.10
lz 0.20-0.22 lo 0.10-0.12 lov 0.13-0.15

REMARKS. I am indebted to Dr A. H. Cheetham, who provided the photographs of Canu's type specimen illustrated here on Pl. 3C, D. They show that the very small zooids have well-preserved orifices and frontal shields, particularly in those of the overgrowth layer. The large foramina

appear in many cases to be bordered by rims of calcification like those of *T. spathulata*, *T. perplexa* and *T. musaica*. The secondary calcified orifice slopes distally toward the basal wall, and there is a distinct, thickened suboral bar, as in many Cribrimorpha. Similar zooids are found in the ancestrular region of other species (see pp. 106, 121 and Fig. 1). Avicularia are small and randomly orientated; the bar is visible in many cases. All the brood chambers are broken frontally; they are raised, 'hyperstomial', and do not appear to have been closed by the operculum.

The exact locality of *T. maçonica* was given as 'Lower Eocene, Djebel Blidji vers le Nord, sur *Ostrea punica*'. Although it seems very probable that other, more southerly African fossil specimens of *T. maçonica* remain to be discovered, none were reported by Gorodiski & Balavoine (1961) from the Eocene of Senegal. No fossil specimens of *Tremogasterina* were found from the Upper Miocene of Loanda by Buge & Galopim de Carvalho (1964).

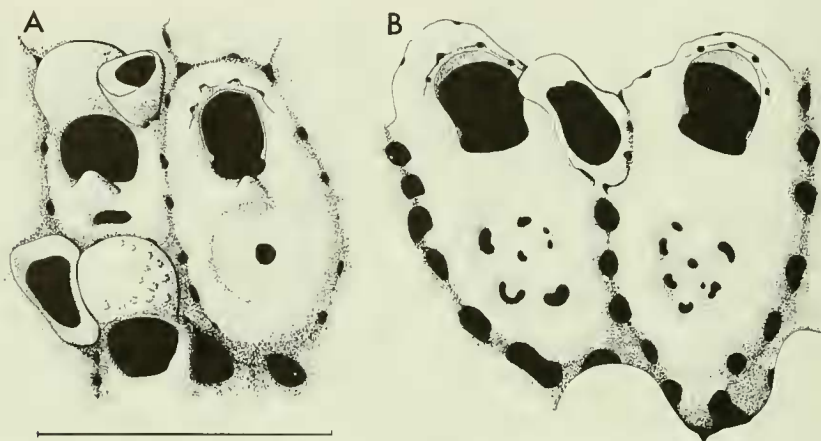


Fig. 6 European Miocene *Tremogasterina*. (A) *T. areolata* (Reuss). Drawn from the type-specimen, NMV, Baden, Austria. Zooids showing elongated orifice, brooding zooids with dimorphic orifices and avicularia incorporated into the calcification of the brood chamber (cf. Fig. 8B, '*T. miocenica*'). (B) *T. pouyetae* sp. nov. Drawn from the holotype specimen, UCB, Hérault, France. Zooids showing elongated orifices and numerous frontal foramina (cf. Pl. 4C). Scale = 0.50 mm.

Tremogasterina areolata (Reuss)

Lepralia areolata Reuss, 1874 : 156, pl. 4, figs 9, 10.

Tremogasterina areolata (Reuss), Canu & Bassler, 1928a : 44. David & Pouyet, 1974 : 112, pl. 6, fig. 7.

MATERIAL EXAMINED. Type. NMV, specimens on *Porites incrustans*, Baden, Austria, Miocene.

DESCRIPTION (Fig. 6A). Colony encrusting. Zooids small with rounded frontal shields. Orifices elongated, with four spine bases and a small proximal mucro present in some zooids. One to four frontal foramina present. Avicularian rostra raised, rounded, occasionally truncate or pointed, randomly orientated, with a bar. Vicarious avicularia present. Brood chambers prominent.

MEASUREMENTS (in mm).

Lz 0.33-0.48 Lo 0.15-0.16 Lov 0.12-0.15 Lr 0.08-0.15

lz 0.28-0.39 lo 0.12-0.13 lov 0.16-0.18 lvic 0.30-0.45

REMARKS. The type-specimens consist of two colonies, one of approximately 2000, the other of approximately 400 zooids. Neither colony has an ancestrular region preserved and there are areas of overgrowths and also microenvironmental changes in shape, size and orientation of zooids, etc., due to crowding by other bryozoan species and irregularities of the substratum. Crowding is caused by colonies of ten other species present, but some uninterrupted growing edges have been preserved. These show that the zooids have one to two distal and two lateral large, chambered

septulae, and twenty-five to thirty frontal septulae which extend round the distal end of the zooids. The frontal calcified shields are inflated, and finely granular; the central areas are slightly depressed, and have one to four foramina. Foramina are most frequently double, or single and trifoliate. Ontogenetic thickening of the frontal shield is not very extensive, and the common funnels between zooids are not separated by prominent bars of calcification. The orifices are distinctly elongated, and in many zooids the paired condyles are expansions from a ridge which is continuous distally below the level of the outer calcification (see Fig. 6A). There are four oral spine-bases and a small proximal mucro is often present. Avicularia occur somewhat irregularly among zooids and are small but very prominent. The subrostral chambers are considerably raised above, and the rostra are parallel to, the level of the zooidal frontals. The distal part of the rostra are usually rounded, but some are broadly truncate and others apparently pointed. The orientation of interzooidal avicularia is very variable, but there is a tendency to be distally or laterally directed. A few examples have a complete bar; in others this may have been broken and worn, and the avicularia appear to have small condyles. Vicarious avicularia are present, but very rare, occurring in the proportion 1 : 500 zooids; they have wide rostra and no bar. Brood chambers are frequent, often occurring in groups; approximately 100 are present. Orifices of brooding zooids are slightly dimorphic, being wider than those of autozooids. The brood chambers are small, finely tubercular and very prominent. A laterally placed avicularium is characteristically incorporated by ontogenetic thickening into the calcification of the brood chamber (see Fig. 6A).

Tremogasterina pouyetae sp. nov.¹

MATERIAL EXAMINED. HOLOTYPE. UCB Bz52 Tourbes: Saint Jean (Hérault), S.W. France, Helvetian, Miocene. Paratypes Bz61 Nezignan l'Eveque (Hérault), Molasse, Marns Sableuse, and Bz42, 43, 44, all Helvetian, Miocene.

DESCRIPTION (Pl. 4C, Fig. 6B). Colony encrusting oyster shell. Zooids large, with inflated frontal shields. Orifice elongated, with condyles and four to six oral spines, but no mucro. Three to eight small frontal foramina. Avicularia raised, with truncate or rounded rostra, usually orientated distally; vicarious avicularia not seen. Brood chambers small, prominent.

MEASUREMENTS (in mm).

Lz 0.42-0.68 Lo 0.16-0.18 Lov 0.20 Lr 0.18-0.24
lz 0.30-0.36 lo 0.12-0.14 lov 0.22

REMARKS. The colonies encrust both the inner and outer sides of oyster shells. There is a total of approximately 5000 zooids present. No ancestrulae are present and areas of overgrowth are common, but the growing edges of the primary lamina are not crowded, although colonies of *Onychocella angulosa* and other species are present. Zooids at the growing edge show that there are one to two distal and two to three lateral chambered septulae, and fifteen to twenty-six frontal septulae. These extend distally round the zooidal orifice. The frontal calcified shield is inflated and the central area depressed, with three to ten rounded or reniform foramina. The orifice is elongated, with paired condyles and four to six oral spines; the distal rim is often distinctly raised and hooded. There is slight ontogenetic thickening of the frontal shield, but no sign of a mucro. Avicularia are rare, occurring with a frequency of 1 : 8-10 zooids in parts of the colonies, although they are more frequent in other areas. They are fairly prominent, the rostra raised and truncate distally in well-preserved examples, rounded in others which appear to be worn. Generally, the majority is directed distally or distal-laterally; a few have a complete bar preserved. Vicarious avicularia are not present. Brood chambers are rare and badly preserved and only three have been seen. They are small and prominent, and the orifices of the brooding zooids are not dimorphic.

Although ancestrular regions are not present, a primary zone of change can be inferred in the holotype. By extrapolation of the existing series of zooids backward down the astogenetic gradient, it is inferred that the zooids belong approximately to the seventh or eighth generation from the origin of the colony. The increase in zooid length is expressed as a series: Lz 0.44, 0.46, 0.48, 0.51,

¹ Named after Mlle S. Pouyet, Université Claude Bernard, Lyon.

0.54, 0.58, 0.60 mm, The primary zone of repetition is established by the twelfth to fourteenth zooid generation from the hypothetical ancestrula. Increase in length of the orifice is expressed as a series: Lo 0.14, 0.16, 0.16, 0.18 mm, . . . , the maximum length being reached by the tenth to eleventh zooid generation. The zooids show the character of the orifice and frontal shield extremely well (see Pl. 4C); the condyles and spine bases, and the funnels between zooids are particularly clear. The zooids near the growing edge also show incipient brood chambers, the earliest appearing at the fifteenth zooid generation from the hypothetical ancestrula.

T. pouyetae differs from both *T. maçonnica* and *T. areolata* in its larger dimensions. It is very similar to *T. areolata*, but has a greater number of frontal foramina, raised distal borders to the orifices and shows no dimorphism in the orifices of brooding zooids.

The *Tremogasterina mucronata*-complex

The populations comprising '*T. mucronata*' appear to fall into three groups which are to some extent correlated in time and space. The eight species described by Canu & Bassler (1923, 1928a, 1928b) from Florida, the Gulf of Mexico and Brazil have been considered to fall within the range of *T. mucronata* (Smitt). These species appear to differ from each other in character states which are the result of astogenetic and ontogenetic stage, or in state of preservation of both fossil and Recent specimens. Great variation in size of zooids and orifices, number and degree of occlusion of foramina, number of spines and in size and shape of avicularia has been found in single colonies from the British Museum (Natural History) and United States National Museum Collections, which included states considered by Canu & Bassler to be specific (see Powell & Cook, 1967). Although some of the fossil populations seem to fall within *T. mucronata*, others, particularly some Miocene forms from North America, possess a correlation of character differences which relate them to the African and European fossil forms, and are therefore here treated as a separate population ('*T. miocenica*'). The Recent forms from the Mexican and Californian coast also show distinct character correlated differences, particularly in the size and shape of the orifices and avicularia, and are here considered to be a separate species, *T. subspatulata*.

a. *Tremogasterina mucronata* (Smitt)

Escharipora (?) *mucronata* Smitt, 1873 : 24, pl. 5, figs 113–115.

Tremogasterina mucronata (Smitt), Powell & Cook, 1967 : 9, pl. 1a, b.

MATERIAL EXAMINED. In addition to the specimens listed by Powell & Cook (1967), three specimens from the USNM collections have been examined (see Appendix, p. 141).

USNM *T. granulata* 'Albatross' Stn 3005; Fowey Light, 72 metres; *Tremogasterina* sp., 'Albatross' Stn. 2319, N. of Cuba.

DESCRIPTION (Pls 1B, C, 5C, 6E, F, Fig. 1E). Colony encrusting sponges, shell, Bryozoa, with unilaminar and bilaminar expansions and overgrowths. Zooids large, sometimes with more than one series of frontal septulae. Orifices with small lateral indentations and very small condyles and two to six oral spines. One to seven frontal foramina, placed in a central depression, becoming occluded wholly or in part during ontogeny. Suboral mucro often well developed. Avicularia very variable in size and shape, usually orientated distally. Rostra typically truncate with a distal expansion, but also acute or rounded, sometimes within one colony. Vicarious avicularia not generally common, but frequent in some colonies. Brood chambers large and wide.

MEASUREMENTS (in mm).

Lz 0.60–1.00 Lo 0.17–0.25 Lov 0.24–0.35 Lr 0.25–0.60

lz 0.35–0.60 lo 0.14–0.24 lov 0.30–0.40 lvic 0.60–0.80

REMARKS. The very large range of variation among the fossil and Recent specimens assigned to *T. mucronata* was discussed by Powell & Cook (1967). The type-specimens of Canu & Bassler's species and much other material in the USNM collections has been re-examined. Some specimens (e.g. *T. ventricosa*) have a large number of small, acute avicularia and there is a tendency in some Miocene forms (e.g. *T. horrida* and *T. truncatorostris*) towards smaller zooids, but the ranges of

variation within colonies, particularly in the often fragmentary type-specimens, is extremely large. Each of the ranges for the twenty-two characters measured or assessed overlaps considerably among specimens, and it appears that ontogenetic and astogenetic differences are responsible in many cases for the very fine specific differences given by Canu & Bassler in the original descriptions. Several specimens were included in the analysis of populations (see Table 2), and these consistently clustered together. Osburn (1940 : 369) listed the records of Smitt (1873) and Canu & Bassler (1928a) in his paper on the Bryozoa of Porto Rico, but had no specimens in his collections. In a later paper, Osburn (1947 : 16) listed specimens from Venezuela which he assigned to *T. granulata*, *T. mucronata* and *T. malleolus* (see Appendix, p. 141).

A colony from the West Indies (BMNH 1931.5.2.6, Kingstown Harbour, St Vincent) has one vicarious avicularium; in addition, dimorphic zooids are present which have an extensive calcified frontal wall with a large, subdivided frontal foramen and frontal septulae. The distal part of the zooid is raised and extended, and the operculum is elongated with a long marginal sclerite and paired, partial medially directed sclerites in the distal part. The cuticle is thicker than that of the autozooidal opercula. The dimensions of these dimorphs, which are not frequent (four dimorphs among approximately 2000 autozooids) are: Lz 0.80–0.90 mm, lz 0.40 mm, L frontal 0.50 mm, Lo 0.28–0.34 mm.

b. '*Tremogasterina miocenica*' populations

Cribrilina miocenica McGuirt, 1941 : 67, pl. 2, figs 10–11.

MATERIAL EXAMINED. BMNH Chipola Formation, Middle Miocene, Florida.

Photographs of specimens from Givhans Bridge, Edisto River, Dorchester Co., S. Carolina, Miocene.

DESCRIPTION (Pl. 4A, B, Fig. 8B). Colony encrusting. Zooids small with flat frontal shields. Orifice with lateral indentations and two to four oral spines. One to four large frontal foramina. Avicularia large, raised, often randomly orientated, but regularly distal in parts of some colonies, rostra slightly expanded distally. Brood chambers prominent.

MEASUREMENTS (in mm).

Lz 0.45–0.50 Lo 0.13–0.16 Lov 0.20–0.25 Lr 0.25–0.45

lz 0.25–0.40 lo 0.15–0.17 lov 0.20–0.29

REMARKS. McGuirt (1941) described specimens from the Middle Miocene of S. Louisiana. The dimensions and general appearance of the photographs of specimens from S. Carolina (on oyster shells) taken by Dr A. H. Cheetham are very similar. The avicularia in McGuirt's specimens were more frequent and more regularly distal in orientation. The specimens from the Chipola Formation (see Scolaro, 1968 : 174) show a great deal of variation in the size and orientation of the avicularia, and have a greater range in size of zooids.

Although larger than the zooids of *T. maçonica*, the proportions of the calcified orifice and brood chamber and the form of the frontal areas are very similar. The similarity in relative size and orientation of avicularia between these specimens and the European Miocene *T. areolata* is also striking. At the same time the fossil specimens have much in common with both fossil and Recent specimens from the American region which are indistinguishable from *T. mucronata*.

c. *Tremogasterina subspatulata* Osburn

Tremogasterina granulata subspatulata Osburn, 1950 : 98, pl. 10, fig. 8.

Tremogasterina granulata magnipora Soule, 1959 : 25, text-fig. 3.

MATERIAL EXAMINED. USC Type-specimens of *T. g. subspatulata* Osburn; Clarion Id, Mexico, Veleró Stn 137–34, 1.5.1934, 104 metres, Nos 1101, 7D11.

Type-specimens of *T. g. magnipora* Soule; Angel de la Guarda Is, Gulf of California, May 1957, 27–31 metres.

USNM *T. g. subspatulata*, Clarion Id.

DESCRIPTION (Pl. 6B, C, D). Colony encrusting sponges and shell, with unilaminar expansions. Zooids of encrusting parts fairly large, zooids of erect parts growing in 'verticillate' lateral rows having smaller dimensions. Orifices large with small lateral indentations and condyles and two to four evanescent spines (seen on very few zooids). No mucro. One to three frontal foramina, often occluded. Avicularia large, with acute rostra orientated distally. Rostra curved downward and finely serrate distally. Vicarious avicularia absent. Brood chambers wide.

MEASUREMENTS (in mm).

Lz 0.42-0.65 Lo 0.22-0.25 Lov 0.22-0.24 Lr 0.30-0.55

lz 0.29-0.34 lo 0.14-0.21 lov 0.30-0.36

REMARKS. The material of *T. g. subspatulata* consists of eight unilaminar, sometimes curved fragments. The specimens of *T. g. magnipora* consist of three fragments, one encrusting shell, the others unilaminar and erect with serpulid tubes and sponges encrusting the basal wall. Together they comprise approximately 600 zooids. Brood chambers are present only in the specimens of *T. g. magnipora*. The characters of the two subspecies seem to be so similar that they may be considered to belong to a single taxon. There are small but consistent differences between them and the specimens assigned to *T. mucronata* from the other side of the Panamanian isthmus. The orifices are larger and the spine bases evanescent and rarely preserved. The avicularian rostra are consistently acute. Some specimens of *T. mucronata* which also exhibit verticillate growth, are, however, very similar in appearance. Until the entire *T. mucronata*-complex can be revised, using more plentiful material, the specimens from California and W. Mexico are here regarded as a distinct species.

Tremogasterina lanceolata Canu & Bassler

Tremogasterina lanceolata Canu & Bassler, 1928a : 48, pl. 13, fig. 9, text-fig. 6A. Powell & Cook, 1967 : 11.

MATERIAL EXAMINED. Listed by Powell & Cook (1967), see also Appendix, p. 141.

DESCRIPTION (Pl. 6A). Colony encrusting coral and other Bryozoa. Zooids large with small, terminal, elongated, sinuate orifices with lateral indentations and condyles large, and five to six spines. Three to eight small frontal foramina. Avicularia very elongated, rounded, orientated distally, with serrate rostra. Mandibles extending beyond the rostrum. Vicarious avicularia absent. Brood chambers prominent.

MEASUREMENTS (in mm).

Lz 0.50-0.85 Lo 0.16-0.18 Lov 0.24-0.28 Lr 0.30-0.55

lz 0.25-0.40 lo 0.10-0.13 lov 0.24-0.30

REMARKS. *T. lanceolata* is here considered to be distinct from *T. mucronata*, although it is possible that specimens from other localities and depths might provide forms intermediate with some included in the *T. mucronata*-complex. The occurrence of two specimens of totally different appearance, from the same locality (Cuba, 146 metres), one assigned here to *T. mucronata* (see Appendix, p. 141), the other to *T. lanceolata* is, however, interesting. The zooids are very elongated, and the frontal foramina small, even early in ontogeny. The foramina are restricted to an elongated, depressed area, rather like that seen in some zooids of *T. pouyetae* (see Pl. 4C). The orifice is very small, with distinct condyles and a slightly sinuate appearance. The operculum which was figured by Canu & Bassler (1928a : text-fig. 6A) also differs considerably from that of both *T. mucronata* and *T. subspatulata*. The frontal septulae do not extend in a series completely round the distal border of the secondary calcified orifice. The avicularia are very long, and the rostra are rounded terminally, raised and serrate distally. The mandibles extend completely beyond the rostra and protrude either into the foramen complex of a distal zooid, or into a gap in the secondary calcification. This gap is presumably produced as the distal frontal shield calcifies, and is a direct result of the presence of the mandible of the proximal avicularium. Similar obstruction of calcification by mandibles has been observed in *T. subspatulata* and in isolated zooids of 'verticillate' colonies of *T. robusta* (see p. 133).

Tremogasterina robusta (Hincks)

Lepralia robusta Hincks, 1884 : 360, pl. 13, fig. 4.

Tremogasterina robusta (Hincks), Powell & Cook, 1967 : 12, pl. 1, figs c, d, text-figs 1-4. Powell, 1967 : 166.

MATERIAL EXAMINED. In addition to that listed by Powell & Cook, 1967 (see Appendix, p. 143). BMNH, Perin Is, Aden, 1966.2.24.1 and 1966.9.2.2, 15 metres.

Gulf of Oman, 1972.7.1.13-16, 18 metres.

? Pleistocene, Givan Peninsula, Red Sea, Reef Limestone, BMNH L51638, 1975.10.4.1, on *Saccostrea* cf. *cucullata* (Born).

DESCRIPTION (Pls 5E, 8B, C, Fig. 1D). Colony encrusting oyster shell and coral, zooids very large. Orifice with lateral indentations and condyles and two (occasionally three) spines. One to three frontal foramina, frequently only one present, tripartite at first, often occluded early in ontogeny. Avicularia large, with asymmetrically curved, slightly spatulate or acute mandibles, orientated distally. Vicarious avicularia rare. Brood chambers not prominent.

MEASUREMENTS (in mm).

Lz 0.60-1.20 Lo 0.24-0.30 Lov 0.20-0.30 Lr 0.40-0.70

lz 0.40-0.65 lo 0.16-0.20 lov 0.30-0.40 Lvic 0.40-0.60

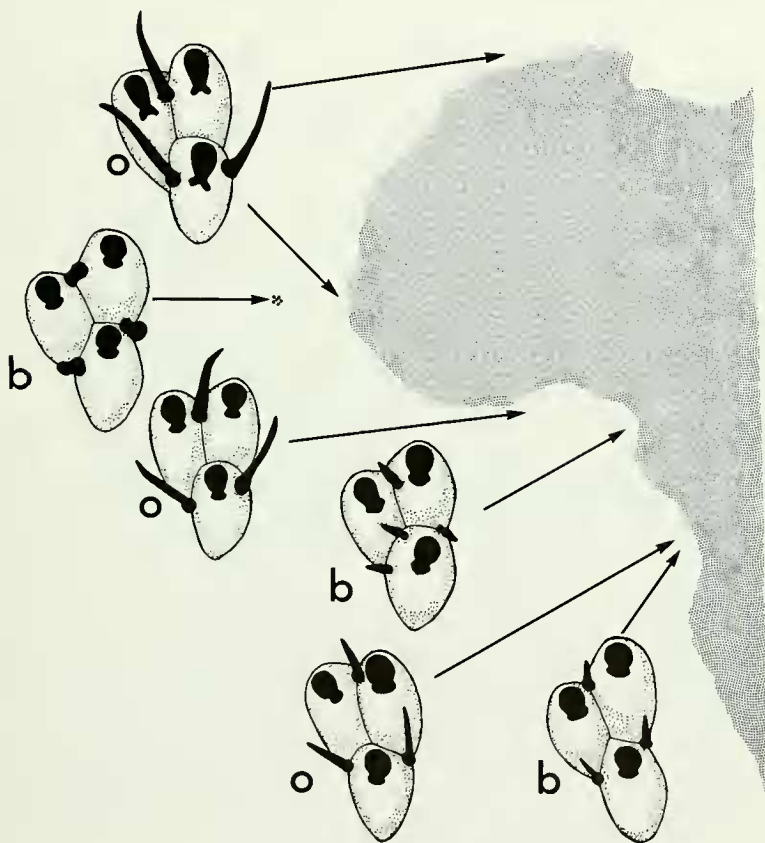


Fig. 7 *T. oranensis* (Waters) and *T. brancoensis* (Calvet). Correlation of orifice shape with avicularium size, shape and orientation; showing distinction in character states between the two 'typical' northern populations of both species, and convergence of states with progressive southerly distribution. (o) *T. oranensis*; (b) *T. brancoensis*.

REMARKS. Recent specimens from the Red Sea have been described in detail by Powell & Cook (1967). Approximately 500 Tertiary oyster and coral specimens in the Palaeontology Department collections at the British Museum (Natural History) have been examined. Many of these show remains of bryozoan colonies, but only one has been found with recognizable colonies of *Tremogasterina* encrusting it. The fossil (? Pleistocene) specimens consist of two colonies encrusting the outer surface of an oyster shell and together comprise approximately 1300 zooids. As many as three laminae are present, most of the overgrowth layers being worn. The zooids are distinctly smaller than those of Recent specimens and show large, chambered distal and lateral septulae and fourteen to twenty well-marked frontal septulae which have developed in many cases into areolae. Few joint funnels have been developed and generally there is little frontal thickening. Many zooids have no apparent frontal foramina, but an equal number have one, oval foramen. The orifices resemble those of Recent *T. robusta* in being slightly elongated, with distinct lateral indentations and condyles; scars of two oral spines are present in three zooids. The avicularia are slightly smaller than those of Recent Red Sea specimens, and the rostra are neither curved nor expanded distally, but acute. Only one, broken, brood chamber has been preserved and vicarious avicularia are apparently absent.

The Tremogasterina oranensis-brancoensis-complex

Examination of material from the regions extending from the north-western African coasts to Angola and the Congo has shown that the populations of these two species exhibit a similarity in character which increases with southerly distribution. The populations do not become indistinguishable, however, and at the extremes of their ranges of variation are completely distinct. They are therefore treated separately.

Preliminary analysis of populations of specimens found in accumulated bottom samples from the Congo and Angola coasts from the Collections of the Muséum Royale de l'Afrique Centrale, and consequent re-examination of material from West Africa, including new collections from Ghana, has shown that *T. oranensis* and *T. brancoensis* are not exclusively allopatric species (cf. Cook, 1964 : 20), and that a third form is present. All three show a progressive degree of similarity in characters associated with the orifice and avicularia. These similarities are also correlated with distribution, and a species complex appears to be present along the north-west to south-west African coasts which requires further investigation.

A summary of the preliminary analysis is given in Fig. 7. Geographically, the Cape Verde Island and Oran-to-Guinea populations comprise two distinct species, *T. brancoensis* and *T. oranensis* respectively. Specimens from the Bay of Biafra, previously assigned to *T. brancoensis*, may be specifically distinct from those from the Cape Verde Islands, but those from the Congo region appear to be intermediate in character. Accompanying specimens of *T. oranensis* from the Congo region, however, also show characters which approach those of the non-typical populations of *T. brancoensis*.

The correlated changes are as follows. In *T. brancoensis* the sinus is rounded in the Congo form, and distinctly elongate and even more rounded in the Bay of Biafra form. The short rounded or oval interzooidal avicularia of the typical population are acute in the other forms, and their orientation becomes more regularly distal. At the same time, vicarious avicularia, which are frequent and conspicuous in specimens from the Cape Verde Islands, become very rare in the Bay of Biafra form, and are apparently absent in colonies from the Congo region. In *T. oranensis*, orifices of colonies from the Congo area show a considerable decrease in the length of the distal part in comparison with the length of the sinus. Concurrently, the proximal edge of the orifice changes from concave in specimens from Senegal to straight in those from Ghana, and to slightly convex in the Congo populations. These orifices are very similar in shape to those of *T. brancoensis* from the same area. The size and shape of the avicularia of *T. oranensis* show a similar series of changes, becoming progressively smaller and less hooked with southerly distribution; until the avicularia of the Congo and Angola populations of both *T. oranensis* and *T. brancoensis* are very alike in size, shape and orientation.

In the absence of fossil specimens, it is impossible to judge whether or not these progressive sequences of correlated differences are indicators of convergence or divergence, or of completely independent environmentally induced reaction.

Tremogasterina oranensis (Waters)

Lepralia oranensis Waters, 1918 : 101, pl. 12, figs 11–13.

Cleidochasma oranense (Waters) Cook, 1964 : 17, pl. 2, fig. 3, pl. 3, fig. 2, text-fig. 6A–B. 1968 : 198, pl. 8, fig. h.

MATERIAL EXAMINED. In addition to that listed by Cook (1964, 1968) material is from bottom samples from Loanda, Congo and Malembe, Angola, from the MAC Collections.

DESCRIPTION (Pls 5F, 7C, D, 8E, F, Figs 1C, 7). Colony encrusting almost any available substratum, often erect and tubular, with multilaminar overgrowths. Zooids small, orifices elongated, with lateral indentations and very large lateral condyles, delineating a proximal sinus which may be concave, straight or convex proximally. There are four oral spines and one to four frontal foramina present very early in the ontogeny, usually occluded later. Avicularia large, with an elongated acute rostrum and a hooked mandible, which is hinged to a complete bar. Vicarious avicularia occasionally present. Brood chambers prominent at first, rapidly becoming immersed by secondary calcification.

MEASUREMENTS (in mm).

Northern specimens:

Lz 0.35–0.52 Lo 0.20–0.24 Lov 0.18–0.22 Lr 0.30–0.45
lz 0.30–0.52 lo 0.11–0.14 lov 0.20–0.23

Ghanaian specimens:

Lz 0.40–0.55 Lo 0.18–0.20 Lov 0.19–0.22 Lr 0.25–0.40
lz 0.38–0.48 lo 0.12–0.14 lov 0.21–0.24 Lvic 0.50–0.65

Angolan specimens:

Lz 0.45–0.55 Lo 0.19–0.21 Lov 0.20–0.21 Lr 0.10–0.30
lz 0.35–0.42 lo 0.14–0.15 lov 0.20–0.24

REMARKS. Examination of additional material collected alive from Ghana has revealed that the early ontogeny of the frontal shield is umbonuloid. The species was previously (see Cook, 1964) assigned to *Cleidochasma*, a genus which has a similar form of orifice, spines and brood chambers. *C. protrusum*, the type-species of *Cleidochasma*, and the widely distributed *C. porcellanum*, both have a cryptocystidean type of frontal wall ontogeny. In addition to its umbonuloid ontogeny, *T. oranensis* possesses all other structures characteristic of *Tremogasterina* as used here.

The earliest stages of zooidal development show an uncalcified anasciform frontal wall, above which develops a typically umbonuloid calcified frontal shield as described on p. 107. The fusion of the distal lateral processes delineates a large elongated oval, the future orifice, and an equally large foramen proximally. The operculum is fully differentiated before this stage, after which the lateral indentations and large condyles are formed, and the proximal foramen becomes rapidly divided and reduced to three to four small irregular or lunate foramina. The occlusion of the foramina follows rapidly (few zooids more than one series proximal to the growing edge show any sign of a foramen). In specimens cleaned with eau de javel, small foramina may still be seen, however, in zooids which have quite thick secondary calcification, and it is probable that, although generally covered by cuticle, and occluded by calcification, some foramina continue to remain uncalcified (see Pl. 8F), or even open. Zooids surrounding the ancestrula in the primary zone of astogenetic change are of interest in that they possess several foramina throughout their ontogeny, and greatly resemble zooids at the same astogenetic stage seen in *T. spatulata* and *T. robusta* (see p. 106, and Fig. 1).

Tremogasterina brancoensis (Calvet)

Lepralia brancoensis Calvet, 1906 : 159, 1907 : 410, pl. 27, figs 7–9.

Cleidochasma brancoense (Calvet), Cook, 1964 : 19, pl. 2, fig. 4, pl. 3, fig. 1, text-fig. 6C–D. 1968 : 199.

Material examined listed by Cook (1964, 1968), see also Appendix, p. 142.

DESCRIPTION (Pls 7A, B, 8D, Fig. 7). Colony encrusting shell, hydroids, rising in erect bilaminar branches, with multilaminar overgrowth. Orifices with lateral indentations and condyles delineating a rounded proximal sinus. Two evanescent spines and one to two small frontal foramina present at earliest ontogenetic stages, the foramina becoming rapidly occluded. Avicularia small, randomly orientated, with a rounded rostrum (in 'typical' form) and mandible hinged to a complete bar. Vicarious avicularia large, spatulate, sometimes common. Brood chambers prominent at first, rapidly immersed by secondary calcification.

MEASUREMENTS (in mm).

Cape Verde Islands specimens:

Lz 0.45-0.75 Lo 0.20-0.22 Lov 0.20-0.24 Lr 0.10-0.25
lz 0.40-0.53 lo 0.14-0.16 lov 0.28-0.30 Lvic 0.40-0.65

Bay of Biafra specimens:

Lz 0.55-0.80 Lo 0.22-0.26 Lov 0.20-0.25 Lr 0.05-0.16
lz 0.35-0.47 lo 0.14-0.16 lov 0.25-0.28 Lvic 0.40-0.60

Angolan specimens:

Lz 0.40-0.53 Lo 0.18-0.20 Lov 0.18-0.22 Lr 0.07-0.14
lz 0.32-0.45 lo 0.14-0.16 lov 0.22-0.25

REMARKS. The series showing the frontal shield ontogeny is not as complete in *T. brancoensis* as in *T. oranensis*, but it is umbonuloid. The proximal foramina are small and evanescent, and rapidly occluded by calcification. One distinctive character of *T. brancoensis* is the relatively random (most frequently lateral) orientation of the interzooidal avicularia. In the 'typical' population, the difference between the mandible shapes of the interzooidal and vicarious avicularia is also striking. *T. brancoensis* also differs from other species in the bilaminar habit. Like those of *T. oranensis*, however, the erect branches are covered by several layers of overgrowth during the later astogenetic stages of colony growth.

As in *T. mucronata*, zooids occasionally develop more than one series of frontal septulae, especially in areas of irregularity in overgrowths.

Tremogasterina celleporoides (Busk)

Lepralia celleporoides Busk, 1884 : 142, pl. 17, fig. 4.

Tremogasterina celleporoides (Busk) Canu & Bassler, 1929 : 118, pl. 12, figs 1-6; Harmer, 1957 : 659, pl. 49, figs 18-21.

MATERIAL EXAMINED. Includes all specimens listed by Harmer, 1957 (see also Appendix, p. 143), and BMNH, China Sea, 1962.2.20.7.

DESCRIPTION (Pls 1A, D, 2, 5D, 8A). Colony encrusting coral and shell, with unilaminar and tubular expansions. Zooids fairly large. Orifices wide, with two to three evanescent spines and small condyles. One to two large frontal foramina, often one tripartite foramen, not often occluded. Avicularia large, with a spatulate mandible orientated randomly. Vicarious avicularia common, often very large. Brood chambers wide.

MEASUREMENTS (in mm).

Lz 0.50-0.70 Lo 0.19-0.22 Lov 0.20-0.30 Lr 0.25-0.40
lz 0.30-0.45 lo 0.18-0.20 lov 0.24-0.36 Lvic 0.60-0.70

REMARKS. *T. celleporoides* forms large, erect colonies with anastomosing, tubular expansions which are multilaminar. It has been described in detail by both Busk (1884) and Harmer (1957).

Tremogasterina spathulata (Canu & Bassler)

Hiantopora spathulata Canu & Bassler, 1929 : 116, pl. 11, figs. 13, 14.

Arachnopusia spathulata (Canu & Bassler), Harmer, 1957 : 657, pl. 68, figs 22, 23, 25, 31.

Tremogasterina spathulata (Canu & Bassler), Powell & Cook, 1967 : 11.

MATERIAL EXAMINED. In addition to that listed by Powell & Cook (1967), see also Appendix, p. 143.

BMNH, Ghardaqa, Red Sea, 1965.9.4.1; China Sea, 1962.2.20.8; South China Sea, DG8, 'Dampier' sample; Aldabra Id, 1971.3.16.1A and 1972.6.1.11; Mahé, Seychelles, 1975.9.24.4.

Professor D. A. Brown Coll. Pliocene, Midway Id, reef, Hole R103-5', No. 152.

Mr R. Day Coll. Recent, Heron Id, south Gt Barrier Reef.

DESCRIPTION (Pl. 5A, Figs 1B, 8A). Colony encrusting shell and coral. Zooids small. Orifice wide, with small lateral indentations and four to five spines. Two to twenty frontal foramina, lunate or irregular, becoming surrounded by funnels of calcification. Avicularia with mandibles expanded and truncate distally, or rounded. Rostra orientated distally or randomly. Vicarious avicularia sometimes present. Brood chambers wide.

MEASUREMENTS (in mm).

Lz 0.40-0.56 Lo 0.10-0.17 Lov 0.19-0.23 Lr 0.10-0.24

Iz 0.30-0.40 Io 0.12-0.14 Iov 0.26-0.30 Lvic 0.40-0.50

REMARKS. The diversity in characters among samples of *T. spathulata* may be related to their wide geographical range, but the correlation is not directly connected with either geographical or bathymetrical distribution. Colonies are usually small and inconspicuous, and some of the samples (e.g. South China Sea, No. 38 and Midway Is, No. 37) consist of one or two small fragments only. The colonies from the Seychelles are slightly larger and differ consistently in several characters. The zooids have a prominent apertural bar with a low mucro and usually only two to four frontal foramina, which are surrounded by a slightly raised, wide funnel of calcification. The avicularia have raised, rounded rostra, quite unlike the truncate, expanded form of most of the other specimens. The general aspect of these colonies is remarkably similar to that of *T. maçonica*, and quite unlike that of the specimens from the Red Sea and Aldabra, which are nearest geographically. Vicarious avicularia are not common and have been found in the samples from the Red Sea and Australia only.

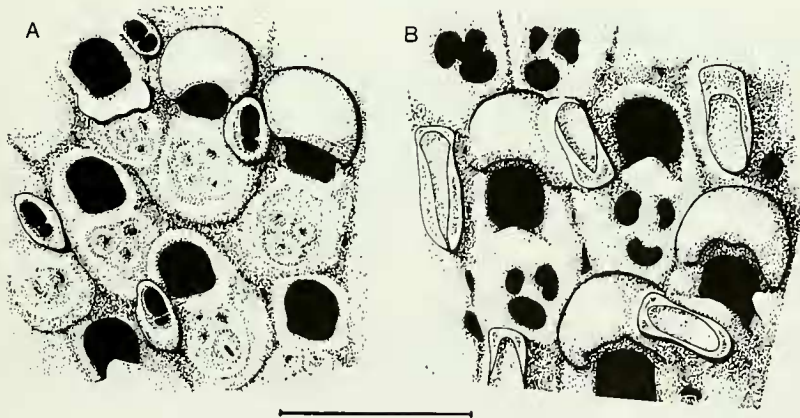


Fig. 8 Recent and fossil *Tremogasterina*. (A) *T. spathulata* (Canu & Bassler), Recent, Seychelles, BMNH, 1975.9.24.4. Zooids, brood chambers and avicularia at a late stage of ontogenetic calcification. Note the unusually small number of frontal foramina, the rounded avicularian rostra and the general similarity with the zooids of the Eocene *T. maçonica* (see Pl. 3C, D and cf. *T. spathulata*, Pl. 5A). (B) '*T. miocenica*', Miocene, Chipola Formation, Florida, BMNH. Zooids, brood chambers and avicularia at a late stage of ontogenetic calcification. Note the general similarity with the zooids of *T. areolata* (see Fig. 6A) particularly in the incorporation of avicularian subrostral chambers in the calcification of the brood chambers. Scale = 0.50 mm.

Tremogasterina perplexa Cook

Tremogasterina perplexa Cook, 1967 : 336, fig. 8. 1968 : 173.

MATERIAL EXAMINED. UMC, Holotype, 'Atlantide' Stn 146, 9°24' N, 14°48' W, 19.4.46, 50–51 metres, 107 F, on shell.

BMNH, 'Calypso' Stn 25, 4°36'5" N, 1°31' W, 24.5.56, 50 metres, C IOU, 1973.3.22.27, on stones.

DESCRIPTION (Pls 1E, 7E, Fig. 1A). Colony encrusting shell and stones. Zooids small, orifices elongated with lateral indentations and six long spines. Seven to fifteen frontal foramina, each often with a unilateral process, secondarily calcified as thickened funnel-shaped expansions, eventually forming blocks of calcifications. Frontal suboral mucro often enlarged. Secondary calcification forming a ridge or hollow, mucronate process, often obscuring the frontal foramina. Avicularia absent. Brood chambers small.

MEASUREMENTS (in mm).

Lz 0.40–0.65 Lo 0.10–0.13 Lov 0.20–0.25

lz 0.26–0.36 lo 0.08–0.10 lov 0.20–0.27

REMARKS. *T. perplexa* was originally described from a single colony. The additional specimens from the 'Calypso' Collection are at an earlier stage in ontogeny, and many zooids have not developed the massive frontal ridges of secondary calcification. These colonies encrust small stones; one consists of twelve zooids, including the ancestrular region, the other is larger, consisting of 120 zooids, some with brood chambers.

The spines are very long, with a sigmoid curve and cuticular base. The opercular sclerite is very long proximally and the two ends extend into the frontal membrane below the edge of the secondary calcified orifice.

T. perplexa differs from all other species of *Tremogasterina* in the complete absence of avicularia. Its known distribution now extends from Guinea to the Ghanaian coast.

*Tremogasterina musaica*¹ sp. nov.

MATERIAL EXAMINED. HOLOTYPE, BMNH, off Ghana, 'deep water' (> 50 metres), 1970.2.8.9.

Paratypes, S36, bottom sample, south west of Tema, Ghana, probably from > 50 metres, 1973.3.22.31.

DESCRIPTION (Pls 1F, 5B). Colony encrusting calcareous accretions and worm-tubes, multilaminar. Zooids small, orifices elongated, with a rounded proximal sinus and distinct lateral indentations and condyles, and four to six oral spines. Eight to fifteen small, lunate frontal foramina. Secondary calcification forming funnels, followed by blocks of calcification. Avicularia small, interzooidal only, with acute mandibles directed distally and slightly laterally and hinged to a complete bar. Brood chambers fairly prominent.

MEASUREMENTS (in mm).

Lz 0.40–0.50 Lo 0.15–0.17 Lov 0.20–0.24 Lr 0.14–0.20

lz 0.30–0.38 lo 0.12–0.13 lov 0.22–0.30

REMARKS. The orifice of *T. musaica* has a distinct rounded sinus, similar to that of *T. brancoensis*, from which it differs in its colony form, frontal calcification, number of spines and lack of vicarious avicularia. It also differs from *T. spathulata* in the shape of the avicularia, and from both *T. spathulata* and *T. perplexa* in the shape of the orifice.

The blocks of calcification surrounding the foramina resemble those found in the later ontogenetic stages of *T. perplexa*, but are not accompanied by the development of large ridges or mucronate processes. The succession of ontogenetic changes in both species is as follows. Lunate foramina become surrounded, either singly or in groups, by funnel-shaped pits with smooth calcification and raised borders (see *T. perplexa*, Pl. 1E). These thicken frontally, and eventually become closely apposed, forming blocks. The marginal frontal septulae apparently remain

¹ Musaicus (L) – mosaic, referring to the appearance of the calcified frontal shield.

capable of transporting nutrients to the hypostegal coelomes during these ontogenetic changes, which are similar to those found in *Exechonella*. Somewhat similar blocks of calcification were reported by Canu & Bassler (1920 : 312) in *Arachnopusia vicksburgica* (see p. 000). If this species proves to be referable to *Tremogasterina* it differs in the size of the zooids, shape of orifice, and apparent absence of spines.

Specimens from the S36 bottom sample include a series of species not generally found in Ghana from less than 50 metres depth. The area south-west of Tema is one where an embayment from deeper water encroaches landward. The material from these sediments is generally, but not exclusively, dead. Much of it is fragmentary and may have been transported. Species found in these samples include *Cupuladria doma*, *Aptonella violacea* and *Cleidochasma rotundorum*.

Acknowledgements

I am indebted to the following colleagues for the loan or presentation of photographs and specimens: Professor D. A. Brown (Australian National University), Dr A. H. Cheetham (U.S. National Museum), Professor L. David and Mlle S. Pouyet (Université Claude Bernard), Mr R. Day (University of Sydney), Drs P. Nuttall and B. Rosen (BMNH), Professor H. Ristedt (Friedrich-Wilhelms Universität) and Drs J. D. and D. F. Soule (University of Southern California). I am also grateful to Mr D. Dean (U.S. National Museum), Mr P. J. Chimonides and Mr J. Brown (BMNH) for their help in the preparation and photography of thin-sections, and to Dr M. Hills (BMNH) for advice on statistical analyses.

Summaries in French and German

Le développement historique de la conception générale de genre *Tremogasterina* a été discuté, et nous donnons ici un aperçu des corrélations des caractères que nous considérons comme typiques de genre ci-dessus. La nomenclature et les affinités du *Tremogasterina* et *Poricella* sont examinés. Nous décrivons ici les régions ancestrales et l'astogénie des zooides, les aviculaires et les chambres d'incubation ('ovicelles'). L'ontogénèse du bouclier antérieur suit le modèle umbonuloïde, dans lequel le pli externe, basiquement calcifié, se développe frontalement envers le mur et l'orifice primaire, qui sont non-calcifiés. Les chambres d'incubation dans *Tremogasterina* sont apparemment les modifications des bourgeons intra-zooidales et frontales. Leur ontogénie est décrite et comparée avec celle découverte récemment dans d'autres genres. La nature de l'ontogénie du bouclier frontal et la convergence de traits morphologiques avec les formes cryptocystidiennes sont pareilles à celle découverte déjà dans Adeonidae et Adeonellidae. L'analyse des populations indique que deux traits divergents dans la zoïde et la structure de la colonie ont pu évoluer depuis le Paléocène. Quinze espèces nominales ou populations sont décrites, dont deux sont considérées nouvelles, et leur distribution dans le temps et l'espace est discutée. Des problèmes de reconnaissance et d'interprétation, particulièrement des échantillons fossiles, sont discutés et des investigations nouvelles ont été suggérées qui puissent fournir des solutions nouvelles.

Die historische Entwicklung des allgemeinen Konzepts der Merkmale der Gattung *Tremogasterina* wird diskutiert, und die Gegenwärtig für diese Gattung als typisch angesehenen Merkmalskorrelationen werden zusammengefasst. Die Nomenklatur und die Beziehung der Gattungen *Tremogasterina* und *Poricella* zueinander werden ebenfalls diskutiert. Die Anzestrularregion und die Astogenie der Zooezien, Avikularen und Brutkammern ('Ovizellen') werden beschrieben. Die Ontogenie des Frontalschildes folgt dem umbonuloiden Muster, bei dem sich eine äussere, basal verkalkte Falte über der primären unverkalkten Frontalwand und dem Orificium entwickelt. Die Brutkammern von *Tremogasterina* sind offenbar modifizierte interzooezielle Frontalknospfen. Ihre Ontogenie wird beschrieben und mit der in jüngster Zeit bekanntgewordenen anderer Gattungen verglichen. Die Art der Ontogenie des Frontalschildes und die Konvergenz der morphologischen Merkmale die Formen cryptocystidien ist den bei den Adeonidae und Adeonellidae gefundenen Verhältnissen analog. Auf Grund der Populationsanalysen erscheint es möglich, dass sich seit dem Paläozän zwei divergierende Trends der Zooezien- und Kolonie-

strukturen entwickelt haben. Es werden fünfzehn nominelle Arten oder Populationen beschrieben, zwei davon neu, und ihre zeitliche und räumliche Verbreitung wird diskutiert. Die Probleme des Erkennens und der Interpretation, besonders von fossilen Exemplaren, wird diskutiert, und weitere mögliche Wege zur Klärung werden vorgeschlagen.

Appendix

The following records of species of *Tremogasterina* have been noted; those plotted on Maps 1 and 2 are marked*.

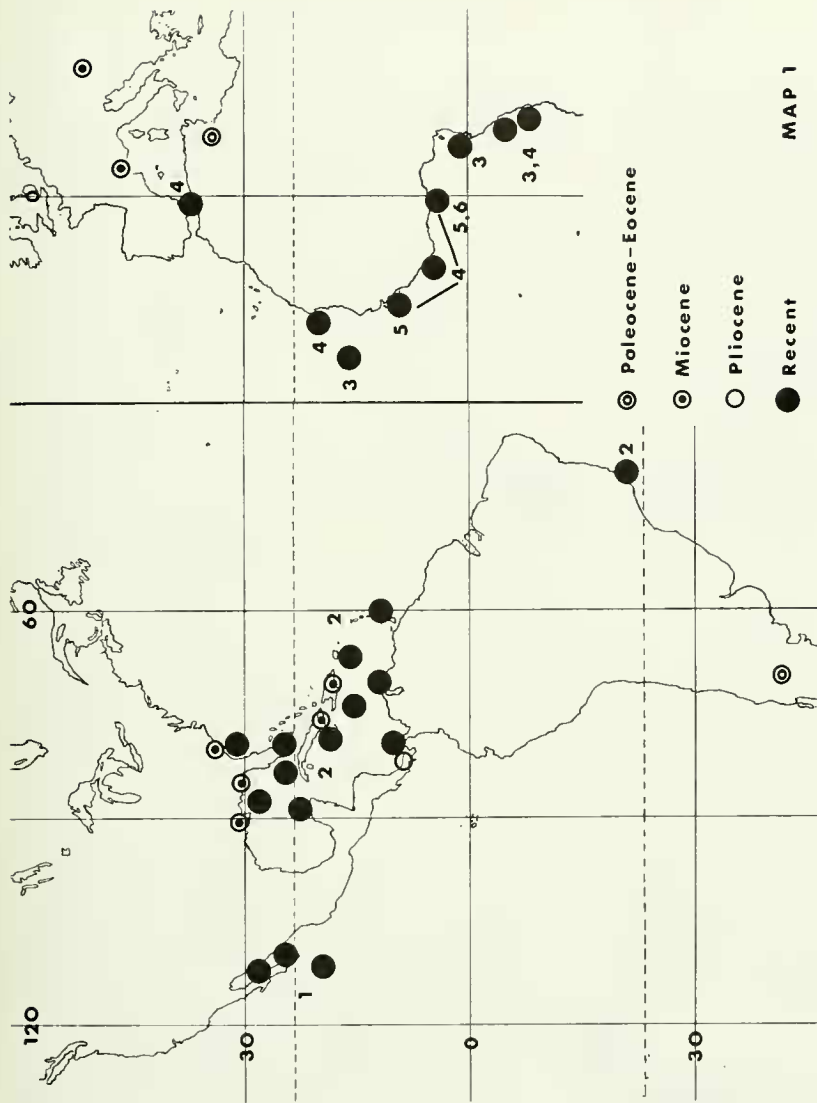
Locality data	Reference	BMNH	Name
<i>Paleocene</i>			
*Argentina	Approx. 39° S, 68° W, Barranca del Jaguel, Neuquén Province	Canu, 1911	<i>T. problematica</i>
<i>Eocene</i>			
*Tunisia	Approx. 34°30' N, 9°00' E, Djebel Blidji ver le Nord, massif ouest de Gafsa	Canu, 1904	<i>T. maçonica</i>
<i>Miocene</i>			
*Austria	Baden	Reuss, 1874	<i>T. areolata</i>
*France	Saint Jean and Nezignan l'Évêque, Hérault		<i>T. pouyetae</i>
*Florida	Jackson Bluff, Ocklocknee R., 25 miles SW of Tallahassee	Canu & Bassler, 1923 (<i>T. horrida</i>)	<i>T. mucronata</i>
Florida	Chipola formation		
*S. Carolina	Givhans Bridge, Edisto R., Dorchester Co.	A. H. Cheetham Coll.	BMNH ' <i>T. miocenica</i> ' ' <i>T. miocenica</i> '
*Louisiana	Core at 7989 ft, Acadia Parish	McGuirt, 1941 (<i>C. miocenica</i>)	' <i>T. miocenica</i> '
*Cuba	Santiago	Canu & Bassler, 1923 (<i>C. cuspidata</i>)	<i>T. mucronata</i>
*San Domingo	Bowden horizon	Canu & Bassler, 1923 (<i>T. truncatorostris</i>)	<i>T. mucronata</i>
<i>Pliocene</i>			
*Panama	Minnitimmi Creek, Bocas Id, Almirante Bay	Canu & Bassler 1928a (<i>T. granulata</i> , <i>T. mal-</i> <i>leolus</i> , <i>T. sparsiporosa</i>)	<i>T. mucronata</i>
*Midway Id	Reef hole, 103.5 ft, No. 152	D. A. Brown Coll.	<i>T. spatulata</i>
? <i>Pleistocene</i>			
*Red Sea	17°06' N, 42°21' E, Gizan Peninsula		1975.10.4.1 <i>T. robusta</i>
<i>Recent</i>			
*W. Mexico	18°20'05" N, 114°44'40" W, 58 metres	Osburn, 1950 (<i>T. g.</i> <i>subspatulata</i>) and USNM	<i>T. subspatulata</i>
Lower California	Angeles Bay	Osburn, 1950 (<i>T. g.</i> <i>subspatulata</i>) and USNM	<i>T. subspatulata</i>
*Bay of California	28°45'30" N, 112°23' W, 36-40 metres and 11 other Stations, 9-84 metres	Soule, 1959 (<i>T. g.</i> <i>magnipora</i>)	<i>T. subspatulata</i>

Locality data	Reference	BMNH	Name
*Bay of California	Espiritu Santo Is, 18-44 metres	Soule, 1959 (<i>T. g. magnipora</i>)	<i>T. subspatulata</i>
Bay of California	25°2'45" N, 110°43'30" W, 38 metres, Albatross Stn 3005	USNM	<i>T. subspatulata</i>
*Gulf of Mexico	Alacran Reef, Campeche Bank		1961.11.2.41 <i>T. mucronata</i>
*Panama	9°36'9" N, 79°40'08" W, North of Porto Bello		1971.3.12.3 <i>T. mucronata</i>
*Gulf of Mexico	28°44' N, 85°16' W, 110 metres, Albatross Stn 2404	Canu & Bassler, 1928a (<i>T. granulata</i> , <i>T. malleolus</i>) USNM	<i>T. mucronata</i>
Gulf of Mexico	Approx. 25° N, 83° W, W. of Tortugas, 66 metres	Smitt, 1873	<i>T. mucronata</i>
Gulf of Mexico	23°10'37" N, 82°20'06" W, 195 metres, Albatross Stn 2319	USNM	<i>T. mucronata</i>
*N. of Cuba	23°10'39" N, 82°18'48" W, 258 metres, Albatross Stn 2320	Canu & Bassler, 1928a and USNM	1932.3.7.61 <i>T. lanceolata</i>
N. of Cuba	Havana, 146 metres		1911.10.1.1713 <i>T. lanceolata</i>
N. of Cuba	Havana, 146 metres		1911.10.1.1692 <i>T. mucronata</i>
Gulf of Mexico	25°04'50" N, 80°15'10" W, 102.5 metres, Albatross Stn 2639	Canu & Bassler 1928a (<i>T. granulata</i>)	1932.3.7.44 <i>T. mucronata</i>
*Off Georgia	31°31' N, 79°05' W, 506 metres, Albatross Stn 2672	Canu & Bassler, 1928a (<i>T. ventricosa</i>)	<i>T. mucronata</i>
*E. Florida	Fowey Light, 15 miles S. of Miami, 73 metres	Canu & Bassler, 1928a (<i>T. granulata</i>) and USNM	<i>T. mucronata</i>
*Jamaica	Discovery Bay, 61 metres		1965.8.2.1, 2 1966.1.6.1 <i>T. mucronata</i>
*W. Caribbean	17°43'40" N, 75°38'25" W, 95 metres, Albatross Stn 2136	Canu & Bassler, 1928a (<i>T. malleolus</i>)	<i>T. mucronata</i>
Gulf of Venezuela	11°30' N, 71° W, 71 metres	Osburn, 1947 (<i>T. mucronata</i>)	<i>T. mucronata</i>
Gulf of Venezuela	12°09' N, 70°31' W, 71 metres	Osburn, 1947 (<i>T. malleolus</i>)	<i>T. mucronata</i>
*Gulf of Venezuela	12°30' N, 70° W, 129 metres	Osburn, 1947 (<i>T. granulata</i>)	<i>T. mucronata</i>
*E. Caribbean	18°30' N, 66°18'50" W, 146-219 metres, Caroline Stn 104	USNM 9766	<i>T. mucronata</i>
E. Caribbean	St Thomas		1840.10.23.82 <i>T. mucronata</i>
E. Caribbean	Kingstown Harbour, St Vincent		1931.5.2.6 <i>T. mucronata</i>
E. Caribbean	Grenada, 211 metres		1911.10.1.1698 <i>T. mucronata</i>
*Brazil	21°48' S, 40°03' W, 128 metres	Canu & Bassler, 1928b (<i>T. malleolus</i>)	<i>T. mucronata</i>
*Cape Verde Is	15°16'34" N, 23°47'44" W, 55-60 metres, Calypso Stn 24	Cook, 1964	1964.9.1.41-43 <i>T. brancoensis</i>
Cape Verde Is	15°16'30" N, 23°47'31" W, 50-65 metres, Calypso Stn 26	Cook, 1964	1964.9.1.44 <i>T. brancoensis</i>

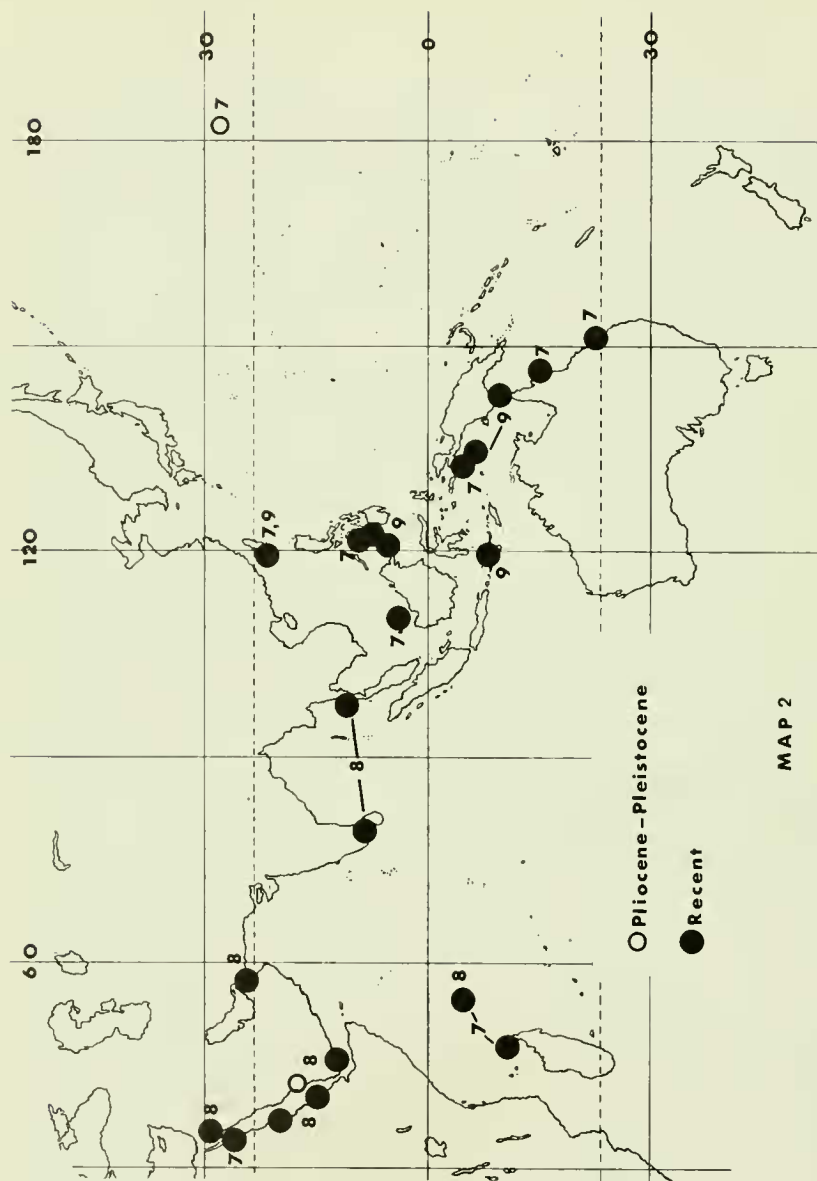
Locality data	Reference	BMNH	Name
*Mauritania	21°05' N, 17°14' W, 43–45 metres, Calypso Stn 1		<i>T. oranensis</i>
Mauritania	22°19' N, 17°05' W, 62 metres, Galathea Stn 4		<i>T. oranensis</i>
Mauritania Mauritania	Cap Blanc, 20–30 metres Cap Blanc, 20–64 metres	Canu & Bassler, 1928c	<i>T. oranensis</i> <i>T. oranensis</i>
Senegal and Guinea	20 Stations, Marche- Marchad Coll. 34–100 metres	Cook, 1964	1921.5.23.7 1927.10.30.11 1964.9.1.37 1970.8.10.9A <i>T. oranensis</i>
Senegal and Guinea	10°22' N, 16°22' W, 41–55 metres, Atlantide Stn 44	Cook, 1968	<i>T. oranensis</i>
Senegal and Guinea	9°23' N, 15°07' W, 30–34 metres, Atlantide Stn 45	Cook, 1968	<i>T. oranensis</i>
*Senegal and Guinea	9°27' N, 14°48' W, 50–51 metres, Atlantide Stn 146	Cook, 1967 and Cook, 1968	<i>T. oranensis</i> <i>T. perplexa</i>
Senegal and Guinea	9°20' N, 14°15' W, 32 metres, Atlantide Stn 145	Cook, 1968	<i>T. oranensis</i>
*Liberia	5°06' N, 9°34' W, 78 metres, Atlantide Stn 60	Cook, 1968	<i>T. oranensis</i>
Liberia Ghana	Petit Tahou 4°43' N, 1°41' W, 46 metres, Atlantide Stn 75	Cook, 1964 Cook, 1968	<i>T. oranensis</i> <i>T. oranensis</i>
*Ghana	4°36'05" N, 1°31' W, 50 metres, Calypso Stn 25	Cook, 1967	1973.3.22.27 <i>T. perplexa</i>
Ghana	5 Stations, Achimota Coll., 0–65 metres	Cook, 1964	1964.9.1.34A, 35, 36 and 1966.1.10.1 1970.2.8.9pt 1973.3.22.31 <i>T. oranensis</i>
Ghana	Off Tema, 50 metres		<i>T. musaica</i>
Ghana	5°37' N, 0°38' E, 28–50 metres, Atlantide Stn 85	Cook, 1968	<i>T. oranensis</i>
*Oran Oran	92–118 metres, 97 metres	Barroso, 1925 Waters, 1918	<i>T. oranensis</i> <i>T. oranensis</i>
*Bay of Biafra	0°25' N, 9°01' E, 73 metres, Calypso Stn 45	Cook, 1964	1964.9.1.38–40 <i>T. brancoensis</i>
Bay of Biafra	2°03' S, 9°01' E, 49–50 metres, Atlantide Stn 123	Cook, 1968	<i>T. brancoensis</i>
*Congo Congo	M'Vassa Landana		1973.3.22.34 1973.3.22.33 <i>T. brancoensis</i> <i>T. oranensis</i>
*Angola	Malembe		1973.3.22.32 1973.3.22.35 <i>T. oranensis</i> <i>T. brancoensis</i>
Angola	Cabinda	Cook, 1968	<i>T. brancoensis</i>
Angola	Ombrizette	Cook, 1968	<i>T. brancoensis</i>

Locality	data	Reference	BMNH	Name
*Red Sea	Ghardaqa	Harmer, 1957	1961.10.30.9, 1965.9.4.1	<i>T. spathulata</i>
*Red Sea	Eilat		1965.8.30.2	<i>T. robusta</i>
*Red Sea	Khor Dongola	Waters, 1909		<i>T. robusta</i>
*Red Sea	Gorgussum and Sheikh Saïd, Massawa, 14-5 metres	Powell & Cook, 1967	1965.2.4.9,11- 14, 1965.8.8. 6-9, 1970.1.4.1	<i>T. robusta</i>
Red Sea	Mersa ar-Rakiyai		1964.7.24.1	<i>T. robusta</i>
Red Sea	E. of Madote Id, 18-36 metres	Powell, 1967		<i>T. robusta</i>
*Gulf of Aden	Perin Is, Aden, 15 metres		1966.2.24.1, 1966.9.2.2.	<i>T. robusta</i>
*Indian Ocean	9°22'35" S, 46°14'41" E, Aldabra Id reef		1971.3.16.1A	<i>T. spathulata</i>
*Indian Ocean	4°30' S, 55°30' E, Mahé, Seychelles		1972.6.1.11	
*Indian Ocean	Seychelles, 22 metres		1975.9.24.4	<i>T. spathulata</i>
Persian Gulf			1882.10.18. 34-41 pt.	<i>T. robusta</i>
*Gulf of Oman	26°10' N, 56°10' E, 18 metres		1889.7.1.5338, 5348	<i>T. robusta</i>
*Ceylon	Gulf of Manaar	Thornely, 1905	1972.7.1.13-16	<i>T. robusta</i>
*Burma	12°30' N, 98°30' E, Mergui	Hincks, 1884		<i>T. robusta</i>
*S. China Sea	5°59' N, 112°35' E 430 metres		DG 8 Dampier	<i>T. spathulata</i>
*S. China Sea	23°32' N, 119°35' E		1962.2.20.8	<i>T. spathulata</i>
*W. Flores	8°30' S, 119°00' E, 0-40 metres, Siboga Stn 50	Harmer, 1957	1962.2.20.7 1961.10.30.11	<i>T. celleporoides</i> <i>T. celleporoides</i>
W. Timor	Hangsisi, Samau Id, 0-36 metres, Siboga Stn 60, 303	Harmer, 1957		<i>T. celleporoides</i>
*Sulu Sea	6°04'30" N, 120°59'30" E, 42 metres, Albatross Stn D5145 and 7 other Stations, 37-420 metres	Canu & Bassler, 1929	1931.12.30.35	<i>T. celleporoides</i>
*Philippines	12°38'15" N, 122°12'30" E, 68 metres, Albatross Stn D5179	Canu & Bassler, 1929		<i>T. spathulata</i>
*Philippines	11°09'15" N, 123°50' E, 58-5 metres, Albatross Stn D5192	Canu & Bassler, 1929		<i>T. celleporoides</i>
New Guinea	1°42'30" S, 130°47'30" E, 32 metres, Siboga Stn 164	Harmer, 1957	1961.10.30.12, 13, 15	<i>T. celleporoides</i>
*Kei Is	4°50' S, 131° E, Tiur Id, 0-54 metres, Siboga Stn 248	Harmer, 1957	1961.10.30.8, 9	<i>T. spathulata</i>
Kei Is	5°30' S, 132°20' E, 22 metres, Siboga Stn 258	Harmer, 1957	1961.10.30.14	<i>T. celleporoides</i>
*Aru Is	5°30' S, 134°00' E, 13 metres, Siboga Stn 273	Harmer, 1957	1961.10.30.16, 17	<i>T. celleporoides</i>
N. E. Australia	Torres Straits, 5-21 metres		1890.3.24.34 1890.4.16.5	<i>T. celleporoides</i>

Locality data	Reference	BMNH	Name
*N. E. Australia 10°30' S, 142°30' E, 14.6 metres, Challenger Stn 186	Busk, 1884	1887.12.9.560- 562, 1944.1.8. 272, 1963.2.12. 281	<i>T. celleporoides</i>
*N. E. Australia Approx. 16°23' S, 14 miles off Queensland coast, Batt Reef, Gt Barrier Reef		1939.2.4.1	<i>T. spathulata</i>
*N. E. Australia 23°25' S, 151°55' E, Heron Id, Gt Barrier Reef	R. Day Coll.		<i>T. spathulata</i>



Map 1 Distribution in time and space of American, West African and European species of *Tremogasterina* (see also Appendix, p. 141). Species-groups with Recent representatives are numbered: (1) *T. subspatulata*, (2) *T. lanceolata* and the *T. mucronata*-complex, (3) *T. brancoensis*, (4) *T. oranensis*, (5) *T. perplexa* and (6) *T. musaica*.



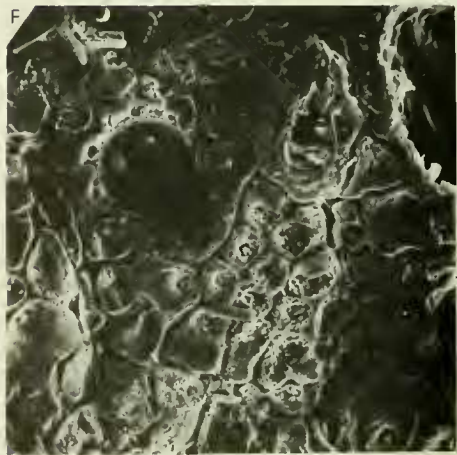
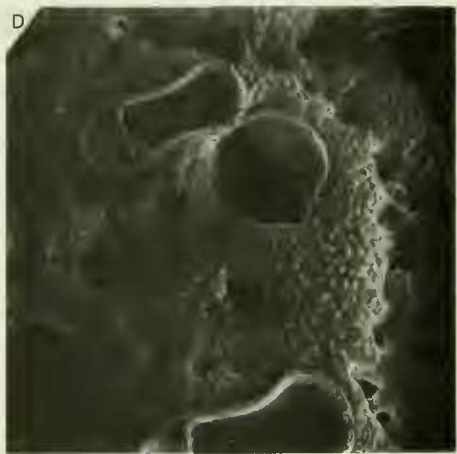
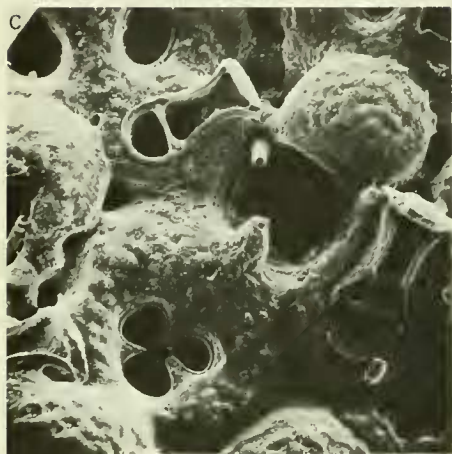


Plate 1 *Tremogasterina* – Astogeny and ontogeny of frontal buds, ontogeny of frontal shield and brood chamber.

- (A) *T. celleporoides* (Busk), Recent, Aru Is, Siboga Stn 273, BMNH, 1961.10.30.16. One of a group of frontally budded zooids. Note areolae developing around and above septulae, and pores in the 'basal' wall derived from interzooidal funnels between two zooids of the primary layer (arrowed). See also Pl. 5D. × 80.
- (B) *T. mucronata* (Smitt), Recent, Kingstown Harbour, St Vincent, BMNH, 1931.5.2.6. Zooids showing late stages of ontogeny of brood chambers. Left hand brood chamber shows the two laminae fusing and is equivalent of Fig. 4F (see p. 112). Right-hand brood chamber is almost completely developed and shows secondary calcification distally (see also Plate 8C). Note spine bases and suboral mucros, and funnel incorporating three areolae (arrowed). × 72.
- (C) *T. mucronata*, as above. Zooid with complete brood chamber. Note similarity of secondary thickening of brood chamber and frontal shield, the spines bases and suboral mucro and relative depression of the trifoliate foramen in the thickened frontal shield. See also Pl. 5C. × 72.
- (D) *T. celleporoides*, as (A) above. Zooid showing increased depth of secondary calcified orifice with frontal thickening. Note interzooidal funnels formed from fusion and frontal extension of areolae, depressed frontal foramina and absence of spine bases. × 63.
- (E) *T. perplexa* Cook, Recent, Ghana, BMNH, 1973.3.22.27. Zooid showing extension of large pits around small frontal foramina as secondary calcification increases. Note spine bases and hollow (broken) suboral mucro. See also Pl. 7E. × 94.
- (F) *T. musaica* sp. nov., Recent, Ghana, BMNH, 1970.2.8.9. Zooid showing thickening of pits into blocks of calcification. Note condyles and sinuate orifice, spines bases and avicularium (at right). See also Pl. 5B. × 96.

All photographs taken using scanning electron microscope.

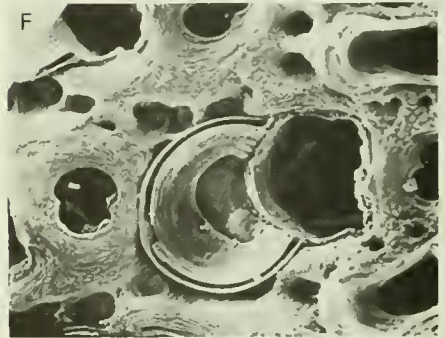
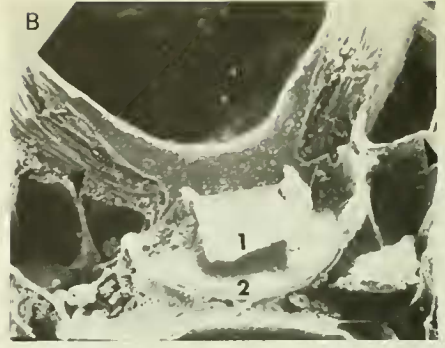


Plate 2 Ontogeny of brood chamber in *T. celleporoides* (Busk), Recent, Torres Straits, BMNH, 1890.3.24.34. Zooids viewed from the distal-lateral side.

- (A) Early stage. First lamina (1) extending distally from maternal zooid, second lamina (2) has just reached the maternal zooid wall, but has grown from the frontal shield of the distal zooid. Note that areolae of sequential zooids (*) are not yet extended and fused to form funnels. Frontal shield of distal zooid only calcified proximally, visible beneath second lamina at bottom of photograph. Equivalent of Fig. 4B. $\times 170$.
- (B) Slightly later stage. Second lamina (2) beginning to curve frontally. Note buttresses of calcification between areolae (arrowed). $\times 187$.
- (C) Later stage. First lamina (1) beginning to curve frontally. Note fusion of areolae to form a funnel (*). Frontal shield of distal zooid damaged. $\times 150$.
- (D) Slightly later stage than C. Both laminae curving frontally. Note buttresses between areolae are visible between the laminae and beneath the second lamina (arrowed). Equivalent of Fig. 4D. $\times 187$.
- (E) Later stage. Note thickening on frontal side of first lamina, and formation of funnels from areolae of the maternal and distal, and the distal and distal-lateral zooids. $\times 75$.
- (F) Later stage. Note close apposition of the laminae prior to fusion, and the distal-lateral funnels marking the opening of the tubular extension of one of the areolae beneath the second lamina. $\times 75$.

For further stages, see Pl. 1B, C, *T. mucronata*.

All photographs taken using scanning electron microscope.

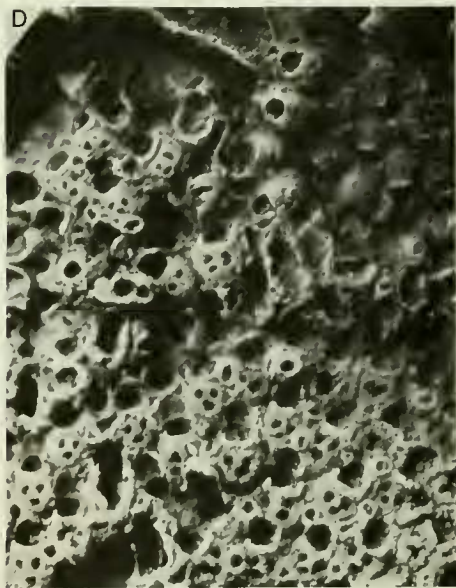
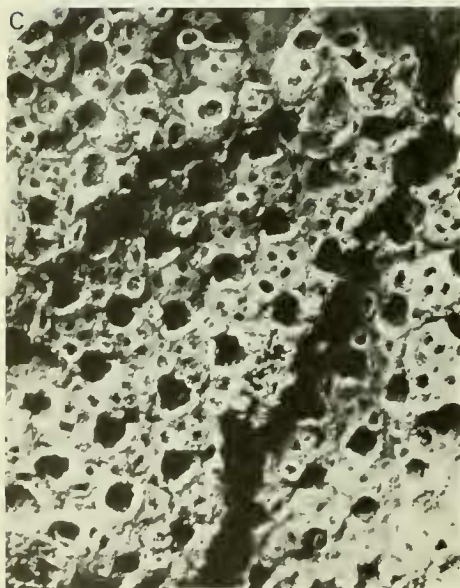
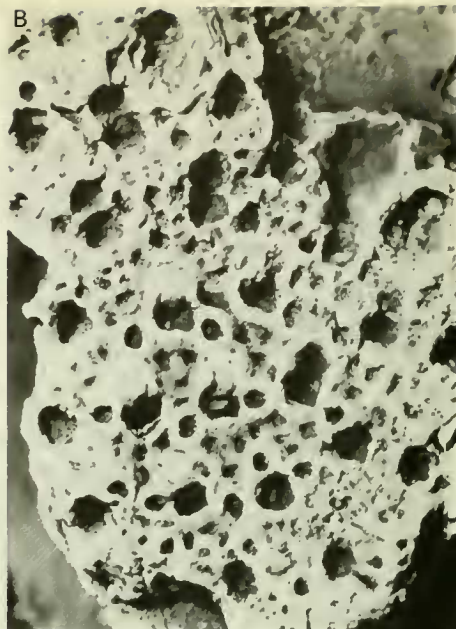


Plate 3 Paleocene and Eocene *Tremogasterina*.

(A), (B) *T. problematica* Canu. Specimen of *Tremogasterina* from Paleocene, Roca Formation, Bertel's locality BJ-7 (see p. 127). Note small zooids, three foramina and avicularia and brood chambers. $\times 38$.

(C), (D) *T. maçonica* (Canu), Eocene, Tunisia. Photographs of type specimen of *Poricella maçonica* Canu from Paris Museum. Note small zooids, prominent apertural bar, three foramina and small, randomly orientated avicularia. In (D) note numerous (broken) 'hyperstomial ovicells' (brood chambers). $\times 38$.

All photographs taken by Dr A. H. Cheetham.

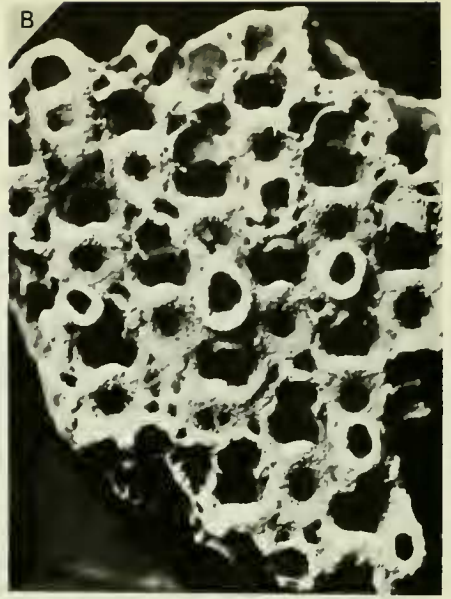
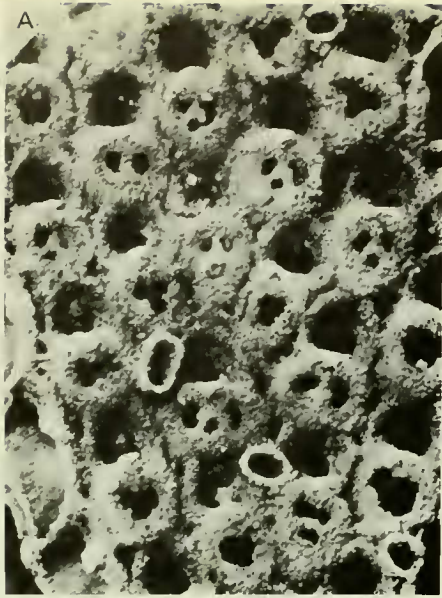


Plate 4 Miocene *Tremogasterina*.

(A), (B) *Tremogasterina* 'miocenica'. Specimen of *Tremogasterina* from Miocene oyster bed, Givhans Bridge, South Carolina, U.S.A. Compare Fig. 8B. Note fairly small zooids, three foramina, raised, randomly orientated avicularia and broken but prominent brood chambers. $\times 39$. (photographs by Dr A. H. Cheetham).

(C) *Tremogasterina pouyetae* sp. nov. Part of the holotype colony, Miocene, Hérault, France. Note excellent preservation, large zooids, elongated orifices and large number of frontal foramina. See also Fig. 6B. $\times 42$ (photograph by P. J. Chimonides).

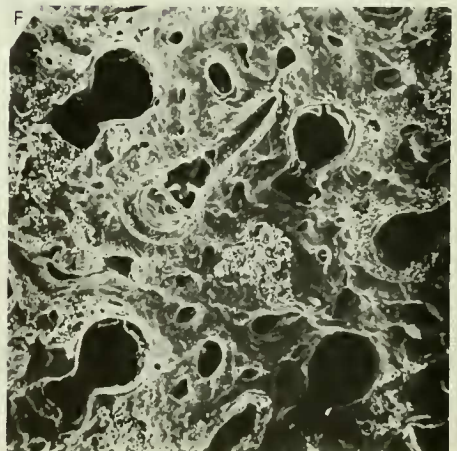
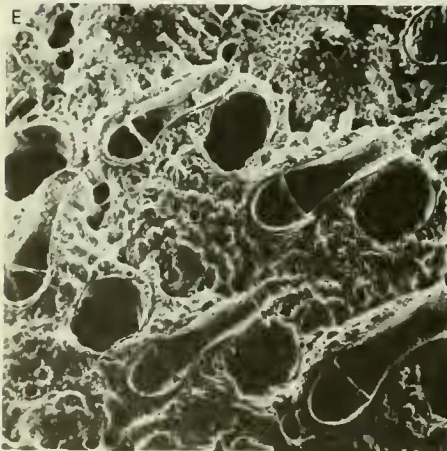
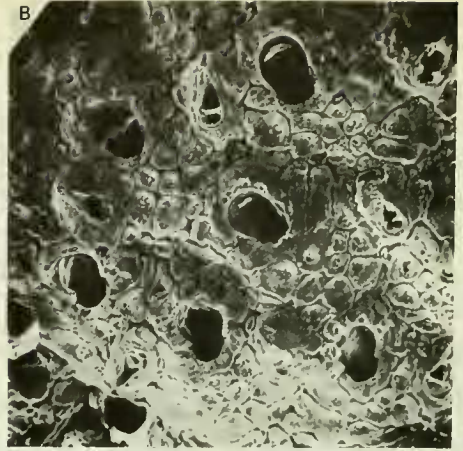


Plate 5 Recent *Tremogasterina*.

- (A) *T. spathulata* (Canu & Bassler), South China Sea, BMNH, 1962.2.20.8. Note large number of frontal foramina, with formation of surrounding funnels, spathulate, truncate avicularia and wide brood chambers. Compare Fig. 8A. $\times 64$.
- (B) *T. nusaica* sp. nov., Ghana, BMNH, 1970.2.8.9. Note the blocks of calcification surrounding the frontal foramina, the sinuate orifices, the spine-bases and small, acute avicularia. See also Pl. 1F. $\times 60$.
- (C) *T. mucronata* (Smitt), Kingstown Harbour, St Vincent, BMNH, 1931.5.2.6. Note the large, trifoliate or paired foramina, the long suboral mucros, the truncate avicularia and brood chambers raised above the secondary calcified orifice. See also Pl. 1B, C. $\times 36$.
- (D) *T. celleporoides* (Busk), Aru Is, Siboga Stn 273, BMNH, 1961.10.30.16. Note the interzooidal funnels and randomly orientated avicularia. See also Pl. 1A. $\times 36$.
- (E) *T. robusta* (Hincks), Gulf of Oman, BMNH, 1972.7.1.13. Note the elongated, slightly sinuate orifices, the small frontal foramina, the spine-bases and very large, asymmetrically developed avicularia. $\times 60$.
- (F) *T. oranensis* (Waters), Senegal, BMNH, 1964.9.1.57. Note the very large condyles, the 'cleithridiate' orifice and the large, acute avicularia. See also Pl. 7C, D. $\times 72$.
- All photographs taken using scanning electron microscope.

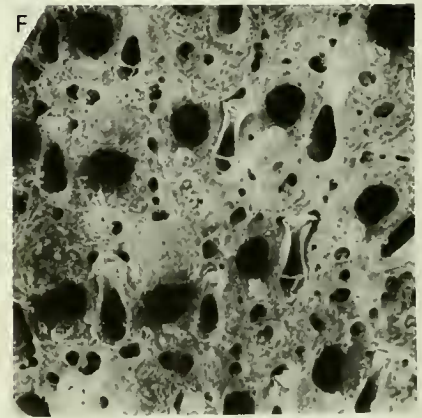
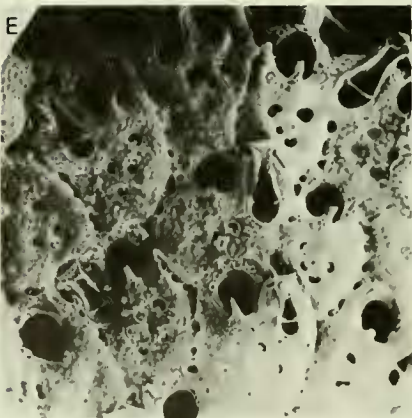
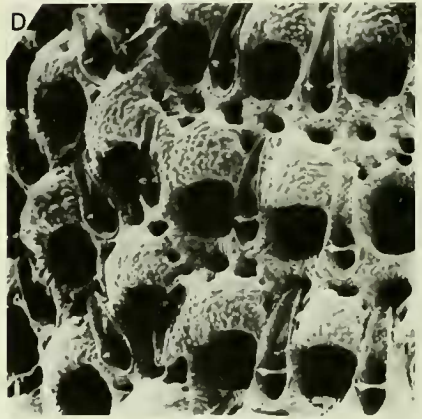
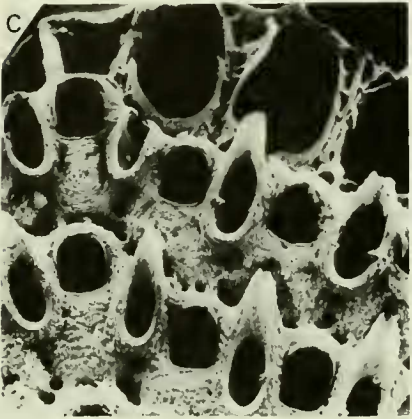
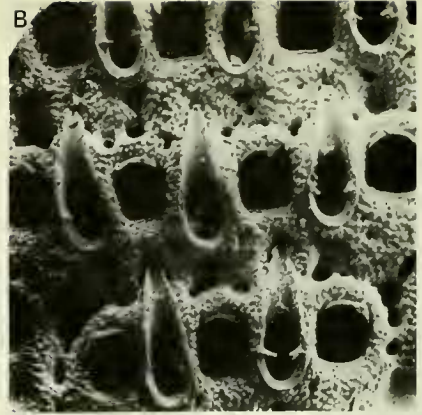
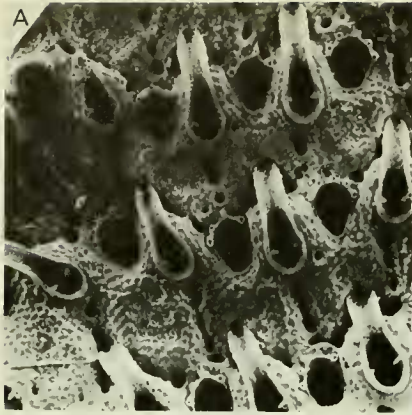


Plate 6 Recent *Tremogasterina* from the American region.

- (A) *T. lanceolata* Canu & Bassler, North of Cuba, Albatross Stn 2320, BMNH, 1932.3.7.61. Note the small, elongated orifices, the numerous but occluded frontal foramina and the large foramina caused by the development of the elongated avicularian rostra. × 43.
- (B) *T. subspatulata* Osburn, part of type material of *T. subspatulata*. Clarion Id, California, USNM. Note 'verticillate' arrangement of zooids and 'lanceolata' development of avicularia. Note spine-bases. × 39.
- (C) *T. subspatulata*, as above. Growing edge, note membraniform zooids, and rapid calcification of previously budded zooid rows, and development of secondary thickening. × 39.
- (D) *T. subspatulata*, Bay of California, Albatross Stn 3005, USNM. Specimen with brood chambers, note smaller, but acute avicularia. × 42.
- (E) *T. mucronata* (Smitt), Discovery Bay, Jamaica, BMNH, 1966.1.6.1. Note the truncate avicularia and very long suboral mucros. × 45.
- (F) *T. mucronata*, Porto Rico, Caroline Stn 104, USNM. Note occlusion of less numerous frontal foramina. × 32.

All photographs taken using scanning electron microscope.

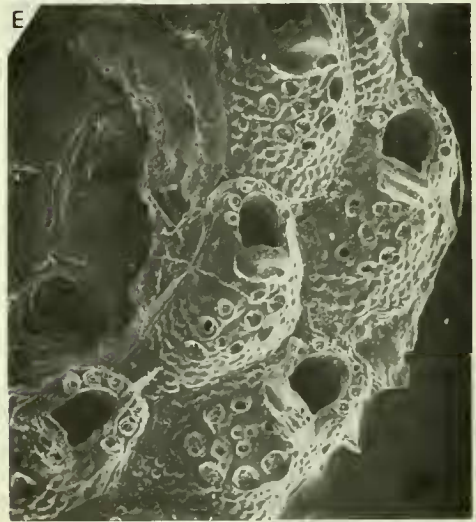
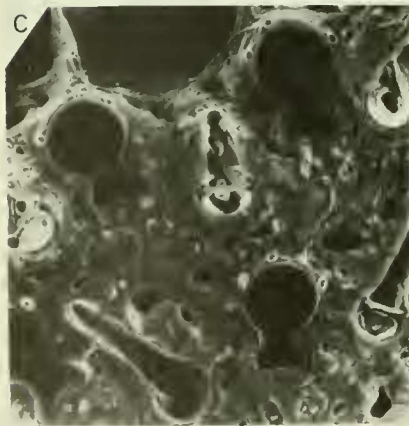
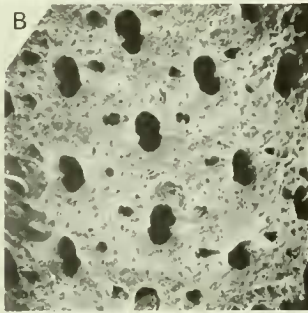
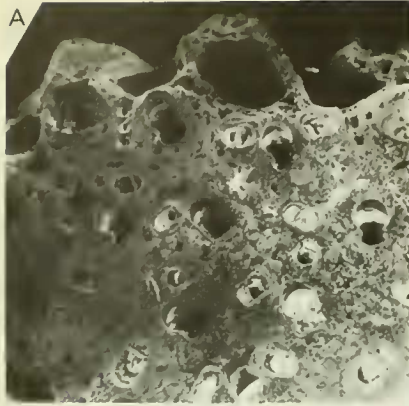


Plate 7 Recent *Tremogasterina* from the west African region.

- (A) *T. brancoensis* (Calvet), Cape Verde Is, BMNH, 1964.9.1.42. Specimen with 'typical' characters of orifice with short sinus and laterally orientated, rounded avicularia. $\times 39$.
- (B) *T. brancoensis*, Bay of Biafra, BMNH, 1964.9.1.40. Specimen with intermediate characters of orifice with deep sinus and laterally orientated, acute avicularia. $\times 35$.
- (C) *T. oranensis* (Waters), Guinea, BMNH, 1970.8.10.9A. Zooids near the growing edge. Note spine-bases and minute frontal foramina. $\times 85$.
- (D) *T. oranensis*, Senegal, BMNH, 1964.9.1.37. Zooid and avicularium at growing edge. Note very thick calcification, lateral areolae and proximal funnels and minute frontal foramina. See also Pl. 5F. $\times 100$.
- (E) *T. perplexa* Cook, Ghana, BMNH, 1973.3.22.27. Zooids growing over *Floridina antiqua*. Note funnels surrounding frontal foramina, spine-bases and suboral thickening preceding growth of mucronate process. See also Pl. 1E. $\times 58$.
- All photographs taken using scanning electron microscope.

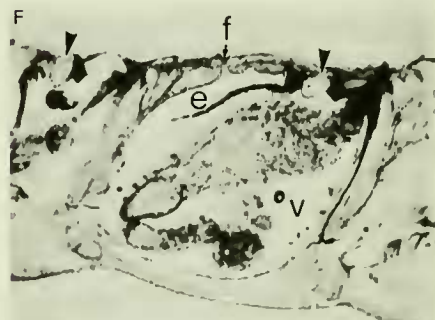
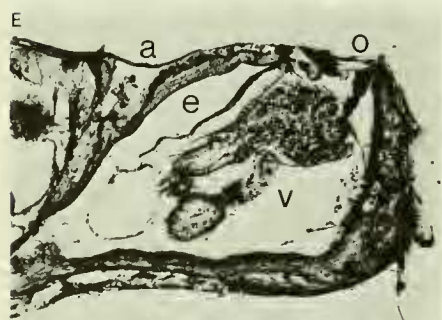
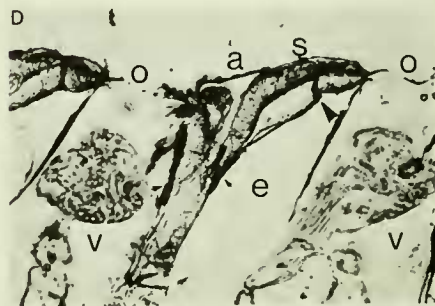
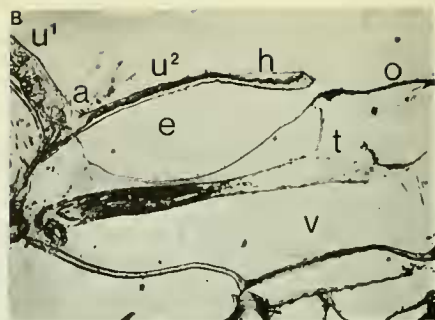
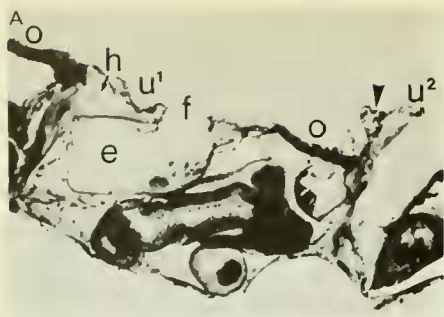


Plate 8 Longitudinal thin-sections of zooids of Recent *Tremogasterina*.

a areola; *e* epistegal space; *f* frontal foramen; *h* hypostegal coelome; *o* operculum; *s* secondary calcification; *t* tentacle sheath; *u*¹ umbonuloid fold proximal zooid; *u*² umbonuloid fold distal zooid; *v* visceral coelome.

Direction of growth arrowed.

(A) *T. celleporoides* (Busk), Kei Is, Siboga Stn 258, BMNH, 1961.10.30.14. Zooid early in ontogeny. Note large frontal foramen and part of umbonuloid fold forming distal part of secondary calcified orifice (arrowed). × 63.

(B) *T. robusta* (Hincks), Gulf of Oman, BMNH, 1972.7.1.13. Zooid early in ontogeny. Note very thin calcification of frontal shield, and compare thickness in part of proximal zooid to left of photograph. × 84.

(C) *T. robusta*, as above. Brood chamber. Compare Fig. 4F. × 75.

(D) *T. brancoensis* (Calvet), Cape Verde Is, BMNH, 1964.9.1.43. Zooids later in ontogeny. Position of septulae at base of areolar tubes (small arrows). Position of frontal foramen passing through primary calcification only (large arrow). × 76.

(E) *T. oranensis* (Waters), Ghana, BMNH, 1964.9.1.35. Zooid near growing edge. Position of condyle (arrowed). × 76.

(F) *T. oranensis*, as above. Zooids later in ontogeny. Note condyles (arrowed) and frontal foramen. × 82.

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